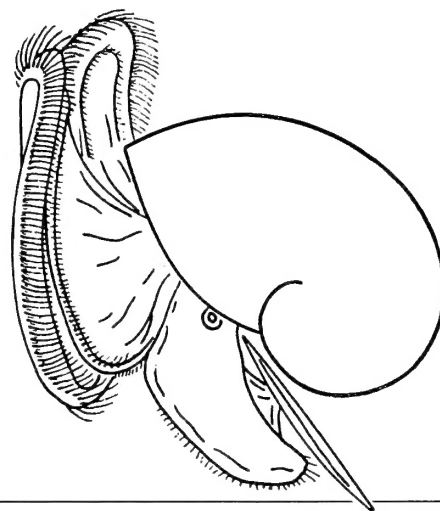


THE VELIGER

A Quarterly published by
CALIFORNIA MALACOOLOGICAL SOCIETY, INC.
Berkeley, California
R. Stohler, Founding Editor



Volume 37

January 3, 1994 to October 3, 1994

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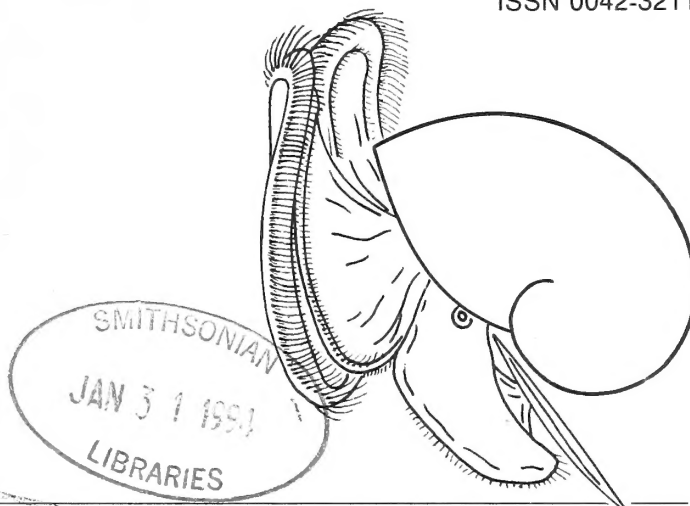
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The Veliger (ISSN 0042-3211) is published quarterly on the first day of January, April, July, and October. Rates for Volume 36 are \$32.00 for affiliate members (including domestic mailing charges) and \$60.00 for libraries and nonmembers (including domestic mailing charges). For subscriptions sent to Canada and Mexico, add US \$4.00; for subscriptions sent to addresses outside of North America, add US \$8.00, which includes air-expedited delivery. Further membership and subscription information appears on the inside cover. The Veliger is published by the California Malacozoological Society, Inc., % Santa Barbara Museum of Natural History, 2559 Puesta del Sol Road, Santa Barbara, CA 93105. Second Class postage paid at Berkeley, CA and additional mailing offices. POSTMASTER: Send address changes to The Veliger, Santa Barbara Museum of Natural History, 2559 Puesta del Sol Road, Santa Barbara, CA 93105.

THE VELIGER

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The Veliger is an international, peer-reviewed scientific quarterly published by the California Malacozoological Society, a non-profit educational organization. *The Veliger* is open to original papers pertaining to any problem connected with mollusks. Manuscripts are considered on the understanding that their contents have not appeared, or will not appear, elsewhere in substantially the same or abbreviated form. Holotypes of new species must be deposited in a recognized public museum, with catalogue numbers provided. Even for non-taxonomic papers, placement of voucher specimens in a museum is strongly encouraged and may be required.

Very short papers, generally not over 750 words, will be published in a "Notes, Information & News" column; in this column will also appear notices of meetings and other items of interest to our members and subscribers.

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Memberships and subscriptions are by Volume only (January 1 to October 1) and are payable in advance to California Malacozoological Society, Inc. Single copies of an issue are US \$25.00 plus postage.

Send all business correspondence, including subscription orders, membership applications, payments for them, changes of address, to: The Veliger, Santa Barbara Museum of Natural History, 2559 Puesta del Sol Road, Santa Barbara, CA 93105, USA.

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International Workshop on the Marine Bivalvia of California

Introduction

by

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In spite of the high species diversity and commercial importance of bivalve mollusks, there appears to be a recent decline in the amount of published research on this fascinating group (Morton, 1992). With this in mind, Brian Morton, Gene Coan, and Paul Scott set about to generate new interest in bivalves, and present an opportunity for many bivalve workers to exchange ideas and techniques. The 1991 bivalve symposium in Berkeley, California, sponsored by the American Malacological Union and the Western Society of Malacologists, was the initial step in bringing researchers together (see proceedings in *American Malacological Bulletin* 9(2):105-215). Following the symposium, the California Malacozoological Society and the Western Society of Malacologists sponsored a workshop at Moss Landing, California from 5-19 July 1991. The eight papers that follow in this issue of *The Veliger* represent research that was begun during the workshop.

Moss Landing was chosen because the great diversity of habitats, coupled with the high productivity of the upwelling system, means that Monterey Bay harbors one of the most species-rich temperate marine faunas. The original buildings of the Moss Landing Marine Laboratories were destroyed in the October, 1989 Loma Prieta earthquake, but a new building is planned for occupancy by 1996. Our workshop was staged in temporary facilities with a fully functional running seawater system.

A dedicated group of 11 bivalve researchers (including two graduate students), representing three countries, attended the workshop. Several local scientists could spend only a few days at the workshop, while our international

and out-of-state guests participated for the duration. The first day was spent on the R/V *Ricketts* collecting bottom samples with a Smith/McIntyre grab and an epibenthic sled. Three stations were occupied at the head of Monterey Canyon, at depths of 30 m, 55 m, and 80 m (Figure 1). Samples were kept in running seawater; participants extracted live bivalves from the sediment, and subsequently sorted and identified all bivalve species collected (Table 1).

Geography and Habitat

Monterey Bay is a broad, almost symmetrical indentation in the central California coast lying between 36.65° and 36.95°N latitude and broadly open to the west. At approximately 37 km north to south and 16 km east to west and covering 550 km², it is the second largest California bay. The most significant feature of the bay is the Monterey Canyon, the deepest and largest submarine canyon along the Pacific Coast of North America. The canyon begins just offshore from Moss Landing and extends in a nearly east-west direction. Within the bay at distances of 14.5 km from shore, the canyon reaches depths of more than 1000 m.

The broad shelf areas north and south of the canyon have substrates of fine sand near shore and sandy mud and mud farther offshore. Substrates in the canyon consist of mud intermixed with rocky outcrops. Intertidally, most of the bay is margined by broad sand beaches backed by sand dunes. At the north and south ends of the bay, rocky

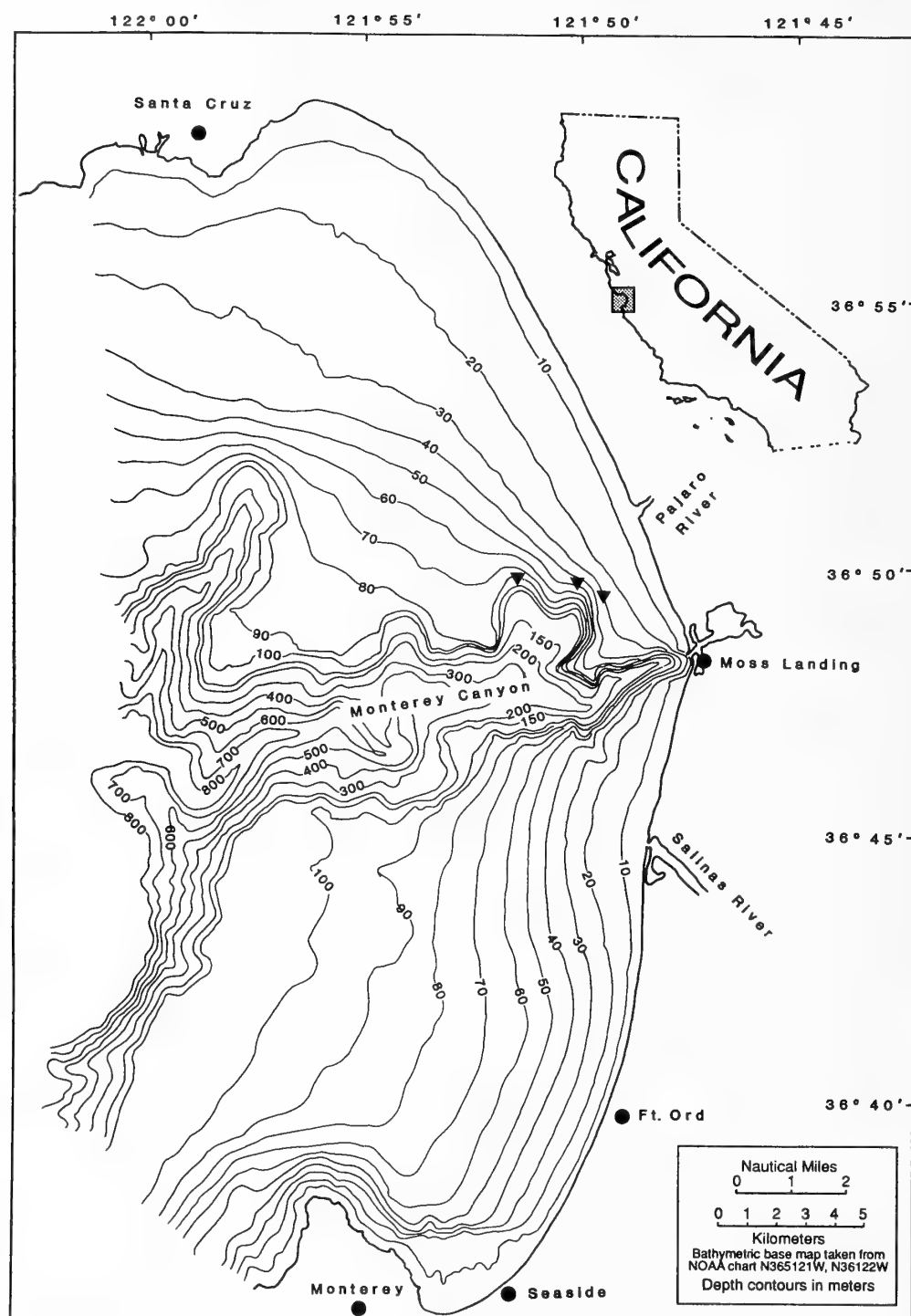


Figure 1

Workshop offshore sampling stations in Monterey Bay, California at 30 m, 55 m, and 80 m.

shores prevail. The southern intertidal rocks are granitic whereas those at the northern end are primarily mudstone and sandstone.

The open conditions of Monterey Bay result in most

areas being subject to considerable wave action, the largest waves coming in the winter storm season.

The water in the bay is cold most of the year due to spring and summer upwelling and the presence of the cool

Table 1

Checklist of Recent Monterey Bay bivalve mollusks collected during workshop. Specimens of the listed species are vouchered at the Santa Barbara Museum of Natural History.

	Collecting sites
Subclass Protobranchia	
Nuculidae	
<i>Acilia castrensis</i> (Hinds, 1843)	80 m
<i>Ennucula tenuis</i> (Montagu, 1808)	80 m
Sareptidae	
<i>Yoldia seminuda</i> Dall, 1871	80 m
Subclass Pteriomorpha	
Mytilidae	
<i>Adula diegensis</i> (Philippi, 1847)	beach drift (shale)
<i>Crenella decussata</i> (Montagu, 1808)	80 m
<i>Modiolus rectus</i> (Conrad, 1837)	80 m
<i>Mytilus galloprovincialis</i> Lamarck, 1819	intertidal (pilings)
<i>Mytilus californianus</i> Conrad, 1837	intertidal (pilings)
Limidae	
<i>Limaria hemphilli</i> (Hertlein & Strong, 1946)	beach drift
Ostreidae	
<i>Ostrea conchalophila</i> Carpenter, 1857	intertidal (estuary)
Pectinidae	
<i>Leptopecten latiauratus</i> (Conrad, 1837)	30 m
<i>Euvola diegensis</i> (Dall, 1898)	30 m
Anomiidae	
<i>Pododesmus macrochisma</i> (Deshayes, 1839)	30 m
Subclass Heterodonta	
Lucinidae	
<i>Parvilucina tenuisculpta</i> (Carpenter, 1864)	55 m
<i>Lucinoma aequizonatum</i> (Stearns, 1891)	55 m
Thyasiridae	
<i>Axinopsida serricata</i> (Carpenter, 1864)	55 m, 80 m
Lasaeidae	
<i>Mysella tumida</i> (Carpenter, 1864)	55 m, 80 m
Carditidae	
<i>Cyclocardia ventricosa</i> (Gould, 1850)	80 m
Cardiidae	
<i>Clinocardium nuttallii</i> (Conrad, 1837)	intertidal (estuary)
<i>Nemocardium centifilosum</i> (Carpenter, 1864)	55 m, 80 m
Veneridae	
<i>Compsomyax subdiaphana</i> (Carpenter, 1864)	55 m, 80 m
<i>Protothaca staminea</i> (Conrad, 1837)	intertidal (sand)
<i>Protothaca tenerrima</i> (Carpenter, in Gould & Carpenter, 1857)	beach drift
<i>Protothaca lacinata</i> (Carpenter, 1864)	intertidal (sand)
<i>Psephidia ovalis</i> (Dall, 1902)	80 m
<i>Tivela stultorum</i> (Mawe, 1823)	beach drift
Tellinidae	
<i>Macoma carlottensis</i> Whiteaves, 1880	55 m
<i>Macoma expansa</i> Carpenter, 1864	beach drift
<i>Macoma indentata</i> Carpenter, 1864	beach drift
<i>Macoma nasuta</i> (Conrad, 1837)	beach drift
<i>Tellina bodegensis</i> Hinds, 1845	55 m, 80 m
Donacidae	
<i>Donax gouldii</i> Dall, 1921	intertidal (sand)
Mactridae	
<i>Sinomactra falcata</i> (Gould, 1850)	25 m
<i>Tresus nuttallii</i> (Conrad, 1837)	intertidal (estuary)
Pharidae	
<i>Siliqua patula</i> (Dixon, 1789)	intertidal (sand)

Table 1

Continued.

	Collecting sites
Corbiculidae	
<i>Corbicula fulminea</i> (Müller, 1774)	beach drift
Myidae	
<i>Cryptomya californica</i> (Conrad, 1837)	beach drift
Hiatellidae	
<i>Hiatella arctica</i> (Linnaeus, 1767)	80 m
<i>Saxicavella pacifica</i> Dall, 1916	55 m
<i>Saxicavella</i> sp. nov.	30 m, 55 m
Subclass Anomalodesmata	
Pandoridae	
<i>Pandora filosa</i> (Carpenter, 1864)	55 m, 80 m
Lyonsiidae	
<i>Lyonsia californica</i> Conrad, 1837	55 m, 80 m
Thraciidae	
<i>Thracia trapezoides</i> Conrad, 1849	80 m

California Current offshore. Surface temperatures range from 10°C to 16°C with the warmer temperatures coming in late summer and fall.

The Bivalve Fauna

Even with a relatively limited effort, collecting during the workshop yielded 43 Recent bivalve species, representing 23 families (Table 1). Our sampling methodology, using an infaunal grab and epibenthic trawl, primarily selected small infaunal heterodont bivalves. The species collected at 55–80 m typify the California continental shelf, an assemblage dominated by veneroid filter-feeders living in fine sediments. Bivalve densities at these depths ranged from less than 1/m² to over 100/m². The coarse, sandy-gravel sediments at the 30 m station produced only four living species, with *Leptopecten latiauratus* (Conrad, 1837) found in high densities. Additional larger species were collected intertidally along the sandy beaches (e.g., *Macoma indentata* Carpenter, 1864) and mudflats (e.g., *Clinocardium nuttallii* (Conrad, 1837)) adjacent to the Moss Landing Marine Laboratories.

The Workshop

The projects undertaken at the bivalve workshop were as diverse as the habitats in Monterey Bay. With a common goal of increasing our knowledge of poorly known eastern Pacific Ocean bivalve species, five participants described the anatomy and functional morphology of selected species. Based on observations and samples from the workshop, one researcher chose to revise a taxonomic complex involving three common eastern Pacific species. One investigator brought previously collected paleontological samples to the workshop in order to obtain assistance in species identification and advice on interpreting the assemblage

represented. Two individuals chose an experimental project that used clams as a prey item of gastropods.

Conclusions

In less than two weeks, our small group of researchers collected the data necessary to describe a new species, detail the functional morphology of four previously unstudied bivalve species, revise a species complex and hypothesize on the evolution of the group, examine bivalve predation by gastropods, and elucidate a previously poorly known Pleistocene deposit in Monterey Bay.

It can easily be argued that in the current climate of financial constraints, inexpensive cooperative efforts like these can provide a wealth of information to the scientific community—not only in terms of the papers published in these proceedings, but also by giving students, young professionals, and established malacologists the opportunity to interact and exchange concepts and techniques. We strongly encourage other malacologists and malacological organizations in the United States and throughout the world to continue this approach of small interactive workshops.

ACKNOWLEDGMENTS

We thank Tracy Thomas and Steven Osborn of Moss Landing Marine Laboratories for enthusiastically assisting with the bivalve workshop. The Moss Landing Marine Laboratories provided sampling time on the R/V *Ricketts*. The California Malacozoological Society and the Western Society of Malacologists generously provided funds to support logistical costs of this workshop.

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International Workshop on the Marine Bivalvia of California

The Biology and Functional Morphology of *Leptopecten latiauratus* (Conrad, 1837): an “Opportunistic” Scallop

by

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Abstract. The byssally attached scallop, *Leptopecten latiauratus*, lives at depths of 0–250 m off the coast of California, attached to a wide variety of substrata. A review of the literature suggests that it is opportunistic in that it settles, in large numbers, on virtually any artificial structure in the sea and on growing kelps (*Macrocystis*). *L. latiauratus* is small (<30 mm in shell height), but matures early, i.e., at a shell height of <5.0 mm. Early energy is therefore put into gonadal development. *L. latiauratus* is a simultaneous hermaphrodite and shows gregarious settlement; both factors aid reproductive success and it thus can occupy a new habitat quickly. It is replaced in the process of succession, typically by mussels, but before being so, has reproduced, the expulsion of gametes probably also being synchronized. Although there is some post-reproductive mortality, many individuals enter a second (and possibly a third) year and continue to reproduce. *L. latiauratus* grows quickly and this fact, in combination with simultaneous hermaphroditism and the life history strategy adopted, identifies it as an *r*-strategist.

Anatomically, *Leptopecten latiauratus* has all the features of a typical pectinid, in terms of shell form, mantle, gill, palp and mouth structure, and stomach architecture. Strong rejectory tracts in the mantle cavity serve to keep it clean in situations where, in the absence of new artificial substrata, *L. latiauratus* must attach naturally to solid objects embedded in a soft substratum. We can conclude, therefore, that the opportunistic *r*-strategy was evolved to allow *L. latiauratus* to quickly colonize ephemeral substrata suitable for byssal attachment.

INTRODUCTION

The Pectinoidea is a globally distributed superfamily of monomyarian bivalves, many of which are of economic significance (scallops), and comprises the extant families Propeamussidae, Entoliidae, Spondylidae, and Pectinidae (Hertlein, 1969). Waller (1991) discussed the evolutionary relationships of the superfamily.

Because of the economic significance of the Pectinidae in particular, there is an extensive literature on scallops, which has been most recently reviewed by Shumway (1991). One of the first detailed descriptions of a scallop, *Pecten maximus*, was by Dakin (1909). Kellogg (1915) described the ciliary currents of the mantle cavity of *Pecten irradians* and *Pecten tenuicostatus* (= *Placopecten magellanicus*), while Drew (1906) described the anatomy of *P. magellanicus*. Yonge (1936) discussed the evolution of the swimming habit in the Bivalvia, most notably the Pectinidae, and

later, Yonge (1953), related such an ability to the evolution of the monomyarian form. A phylogenetically older sister group of the more modern, coastal scallops are members of the deep-water Propeamussidae (Waller, 1971, 1978), some of which can swim, e.g., *Propeamussium*, and are predators of epibenthic zooplankters, e.g., *P. lucidum* (Morton & Thurston, 1989). Not all scallops are free-living, however, and in the deep seas, species of *Cyclopecten* attach by byssal threads to any solid object (Knudsen, 1970). This is also true of many shallow-water pectinids, e.g., *Chlamys* spp. *Hinnites multirugosus* is byssally attached as a juvenile and cemented as an adult (Yonge, 1951), while representatives of the Spondylidae are cemented to the substratum (Yonge, 1973). *Pedum* is thought to bore into corals (Yonge, 1967; Kleemann, 1990), although Waller (1972) believes that this pectinid becomes enclosed by its host coral through a combination of shell and coral growth. The commonest scallops, worldwide,

however, are the small byssally attached members of the Pectinidae, e.g., *Hinnites* and *Chlamys* (Yonge, 1951, 1981). Yonge (1951) described the anatomy of *Hinnites multirugosus*, also from the coast of California, and later (Yonge, 1981) reviewed structure in the Pectinoidea. This is a study of the anatomy of *Leptopecten latiauratus* undertaken at the Moss Landing Marine Laboratories during June/July 1991. Although there is much information on the biology of this species, it has never been married to an anatomical description to provide an overall view of this common Californian pectinid.

MATERIALS AND METHODS

Specimens of *Leptopecten latiauratus* were obtained from between 30–80 m depth off the coast of California at Moss Landing using a small biology trawl (Menzies, 1962) operated from the R/V *Ricketts*.

Living individuals were maintained in running seawater at ambient temperature. The shell heights of all collected individuals plus empty valves were measured to the nearest 0.5 mm using digital calipers. Wherever possible, five individuals of each 1 mm size class were sectioned through the center of the visceral mass to determine the stage of gonadal development using the five criteria of: (1) primordial; (2) developing; (3) maturing; (4) mature and (5) spent, which have been adopted in previous studies of bivalve gametogenesis (Morton, 1982a). Such material and other individuals destined for more detailed histological examination were fixed in 5% formaldehyde and, following routine procedures, were sectioned at 6 μ m with alternate slides being stained in either Ehrlich's hematoxylin and eosin or Masson's trichrome.

Following dissection under a microscope, the ciliary currents of the organs of the mantle cavity and stomach were determined by application of carmine in seawater. Reference specimens of *Leptopecten latiauratus* have been lodged in the collections of The Natural History Museum, London, U.K. (Ref. Nos. 1992082; 1992083; 1992084).

RESULTS

Taxonomy

The genus *Leptopecten* Verrill, 1897, belongs to the Pectinidae Rafinesque, 1815 (Chlamydiae Korobkov, 1957) and is placed in the *Chlamys* Group (Hertlein, 1969) with *Pecten monotimeris* Conrad, 1837 (= *P. latiauratus* Conrad, 1837) as the type species. The genus, known from the Miocene, is mostly confined to warmer seas, but *L. latiauratus* occurs in the northeastern Pacific, along the coast of California, in cold waters. Grau (1959) provided a key to the species of *Leptopecten* of the eastern Pacific.

Biology

Leptopecten latiauratus is widely distributed along the coast of California and Mexico and occurs at depths ranging from just below low tide to 229 m (Grau, 1959). The

individuals reported upon were obtained from depths of between 30–80 m off Moss Landing. Living and empty left valves of these individuals were measured along their greatest shell heights. The results show (Figure 1) that empty valve heights seem to form a peak at between 6.5–8.5 mm, while living individuals show a peak at ~10 mm. On the same figure is indicated the prevalent stage of gonadal development for living individuals as indicated from sections of five individuals of each 1 mm shell height class. Small individuals of between 5.5–7.5 mm were mature, whereas older individuals of between 7.5–8.5 mm were spent. Individuals of between 8.5–10.5 mm were maturing, while those of between 10.5–12.5 mm were mature. There thus seems to be two peaks of mature individuals which coincide approximately with (a) the peak of, albeit slightly larger (and thus gametogenetically spent), empty valves and (b) the peak of larger living (mature) individuals. An interpretation of Figure 1 will be discussed.

Functional Morphology

The living animal: Detached and lying on its side in a bowl of cold seawater, an individual of *Leptopecten latiauratus* relaxes quickly (Figure 2). The foot is extended anteriorly and probes for purchase, followed by locomotory activity. Within a few hours, new byssal threads are secreted.

The mantle is extended from between the shell valves, exposing a number of tentacle groups. Long, primary tentacles arise from the approximate marginal position of each rib on each valve and are interspersed with shorter, secondary tentacles. Also arising from the approximate marginal position of each rib, but also elsewhere, are distinctive pallial eyes. Normally, in such an orientation, left and right inner mantle folds, which form the velum, cannot be seen, but posteriorly are extended and form a simple exhalant siphon. Since there is no pallial fusion to delineate the "siphon," however, it is better termed an exhalant aperture. A powerful jet of water is expelled from the aperture, whereas elsewhere along the mantle margin, water is pumped inwards.

Occasionally, *Leptopecten latiauratus* may make brief attempts at more active movement by pumping jets of water from the mantle cavity at the bases of the anterior and posterior auricles (Figure 3C). This represented simple attempts at swimming, but I was consistently unable to make individuals swim for more than two or three shell adductions, resulting in poor locomotion that cannot be defined better than an escape response. *L. latiauratus* can, however, locomote effectively using its foot.

The shell: The shell of *Leptopecten latiauratus* (Figure 3) has been described briefly by Grau (1959), Morris et al. (1980), and Moore (1984) and is typically scallop-shaped, i.e., approximately circular, thin, and slightly inequivalve. It is reported to attain a shell height of 32 mm (Moore, 1984), although other authors suggest a maximum height of 20 mm (Grau, 1959; Morris et al., 1980). Largest individuals obtained for this study were 14 mm in shell

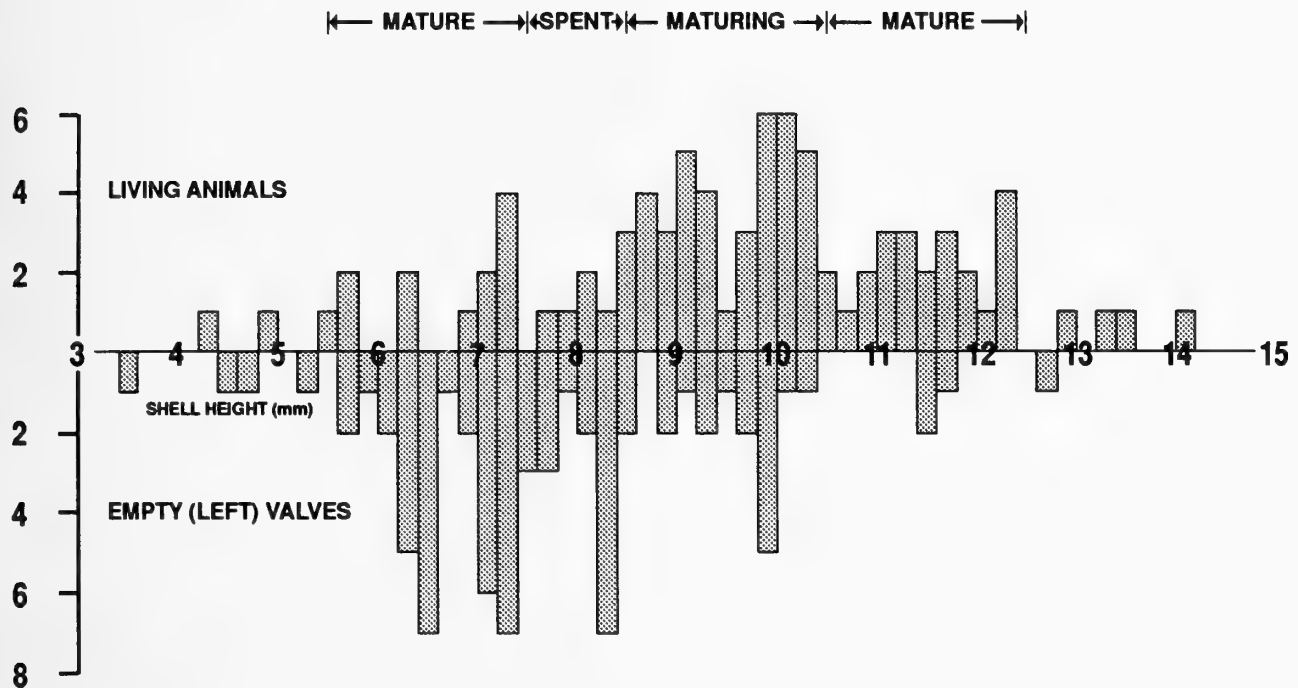


Figure 1

Leptopecten latiauratus. The shell heights of living individuals and empty (left) valves comprising the sample obtained during the course of this study. The overall stage of gonad development of five individuals comprising each 1 mm size class within the living population is also indicated.

Explanation of abbreviations used in figures. A, anus; AOLL, anterior outer ligament layer; AU, auricle; ASO, abdominal sense organ; BG, byssus and byssal gland; C, cilia; CA, statocyst capsule; CG, ciliated groove; CS, crystalline style; CSMG, conjoined style sac and mid gut; CT, ctenolium; DD, digestive diverticula; DD¹⁻⁴, ducts of the digestive diverticula; DH, dorsal hood; DK, distal limb of the kidney; EA, exhalant aperture; FC, food-sorting caecum; G, gonopore; GS, gastric shield; H, heart; ID, inner demibranch; IES, inter-epithelial space; IG, intestinal groove; ILL, inner ligament layer; ILP, inner labial palp; IMF, inner mantle fold; LAP, labial palp; LIP, lips of mouth; LP, left pouch; LPRM, left pedal retractor muscle; LS, left statocyst; M, mouth;

MG, mid gut; MT, minor typhlosole; NF, nerve fibrils; NVG, nerve to visceral ganglia; O, oesophagus; OD, outer demibranch; OLP, outer labial palp; OMF, outer mantle fold; OV, ovary; P, periostracum; PAID, point of attachment of the inner demibranch to the visceral mass; PA(Q), posterior adductor muscle ('quick' component); PA(S), posterior adductor muscle ('slow' component); PE, pallial eye; PG, pedal ganglia; PK, proximal limb of the kidney; PN, pallial nerve; POLL, posterior outer ligament layer; PPG, posterior pallial gland; PR, prismatic shell stage; PRM, pallial retractor muscle; PT¹, major pallial tentacle; PT², minor pallial tentacle; R, ridge on dorsal wall of stomach; RA, renal aperture; RE, rectum; RM, retractor muscle; RPA, renopericardial aperture; RS, right statocyst; RT, retractor tract of mantle; SA, sorting area of stomach; SA⁴, sorting area⁴ of stomach; SEC, secretory cell; SEN, sensory cell; ST, statoconia; SUC, supporting cell; T, major typhlosole; TE, testis; V, ventricle; VT, velar tentacle.

height, although the collections of the United States National Museum contain a specimen of 46 mm shell height and 35 mm individuals are not uncommon (T. R. Waller, personal communication). The shell valves are distinctly inequilateral, not only in terms of the anterior and posterior auricles, but because of a pronounced shell obliquity (Figure 3A, B). The shell is, moreover, only moderately convex, the convexity of left and right valves being approximately the same (Figure 3C, D). Each valve is strongly radially ribbed, the number varying between 12–16 (Grau, 1959), all interspersed by grooves of about equal width. Left and right ribs and grooves interlock marginally forming a distinctively scalloped margin. Beyond the distinctive prismatic stage (Figure 3, PR), the shell is concentrically lamellate, which sometimes results in the formation of distinct scales or spines.

The anterior auricles of both valves are longer than the posterior, and the former project slightly beyond the anterior shell margin. Each auricle also has four to eight riblets. The hingeline (Figure 3E, F) is straight but slightly corrugated by the fine, scale-like, concentric lamellae. The larger anterior auricle of the right valve is more deeply indented than that of the left; at this byssal notch, the byssus emerges from the foot. The ventral border of the byssal notch of the right shell valve of *L. latiauratus* bears a ctenolium (Figure 3A, CT) comprising ~13 pointed teeth which, according to Waller (1984), serves to separate the byssal threads for securer attachment.

A feature commented upon by all previous authors is the wide variability in shell color of *Leptopecten latiauratus* from white, pale yellow, yellow-brown, orange, red, and brown, although, more usually, the shell is either mottled

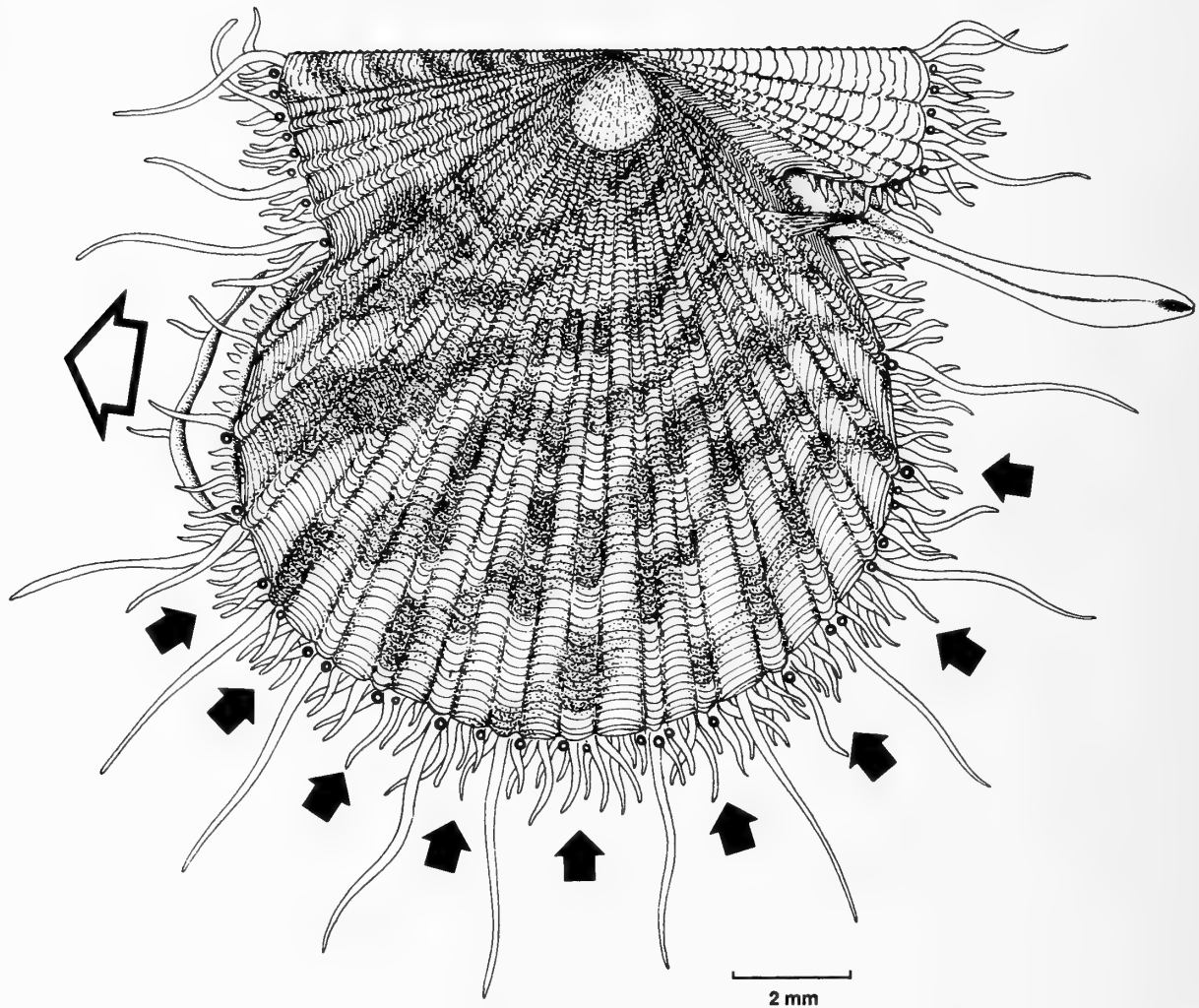


Figure 2

Leptopecten latiauratus. An intact individual as seen from the right side with foot extended and inhalant and exhalant currents indicated by arrows.

or maculated with either white or brown chevrons. Figure 2 illustrates an individual with diagonal rows of brown markings on a paler background. Photographs of a variety of color forms of *L. latiauratus* are given in Coe (1932), Grau (1959), and Clark (1971). An ecomorph, *L. l. monotimeris*, which typically attaches at shallow depths to kelp, is often thinner, with more oblique valves than *L. l. latiauratus* (Grau, 1959). Clark (1971) investigated growth changes in morphology from a typical *L. l. latiauratus* form to that associated with *L. l. monotimeris* and concluded that temperature was responsible. Such evidence is not, however, conclusive, and the factors controlling ecomorphism in *L. latiauratus* need further investigation which, unfortunately, this brief research visit did not permit.

The hinge and amphidetic ligament of *Leptopecten latiauratus* (Figure 3E, F) is typical of the Pectinoidea, first described by Trueman (1953) for *Pecten* and subsequently

by Alexander (1966), Yonge (1975), and Waller (1978). The central, pyramidal inner ligament layer (ILL) is relatively large and located on resilifers. The anterior (AOLL) and posterior outer ligament layers (POLL) extend as a thin, dark line along the dorsal margin of the valves and are overlain by a thin periostracum. Rows of fine, vertically aligned teeth also extend along the dorsal margins of both valves, underneath the outer ligament layers.

The dorsal margin of the right valve interlocks beneath the dorsal margin of the left valve as illustrated in Figure 3C and as is typical of other scallops, e.g., *Propeamussium lucidum* (Thayer, 1972; Morton & Thurston, 1989). Anteriorly and posteriorly, there are small auricular gapes.

The musculature: The musculature of *Leptopecten latiauratus* is much simplified and comprises a single enlarged posterior adductor muscle (Figure 7), which is divided into

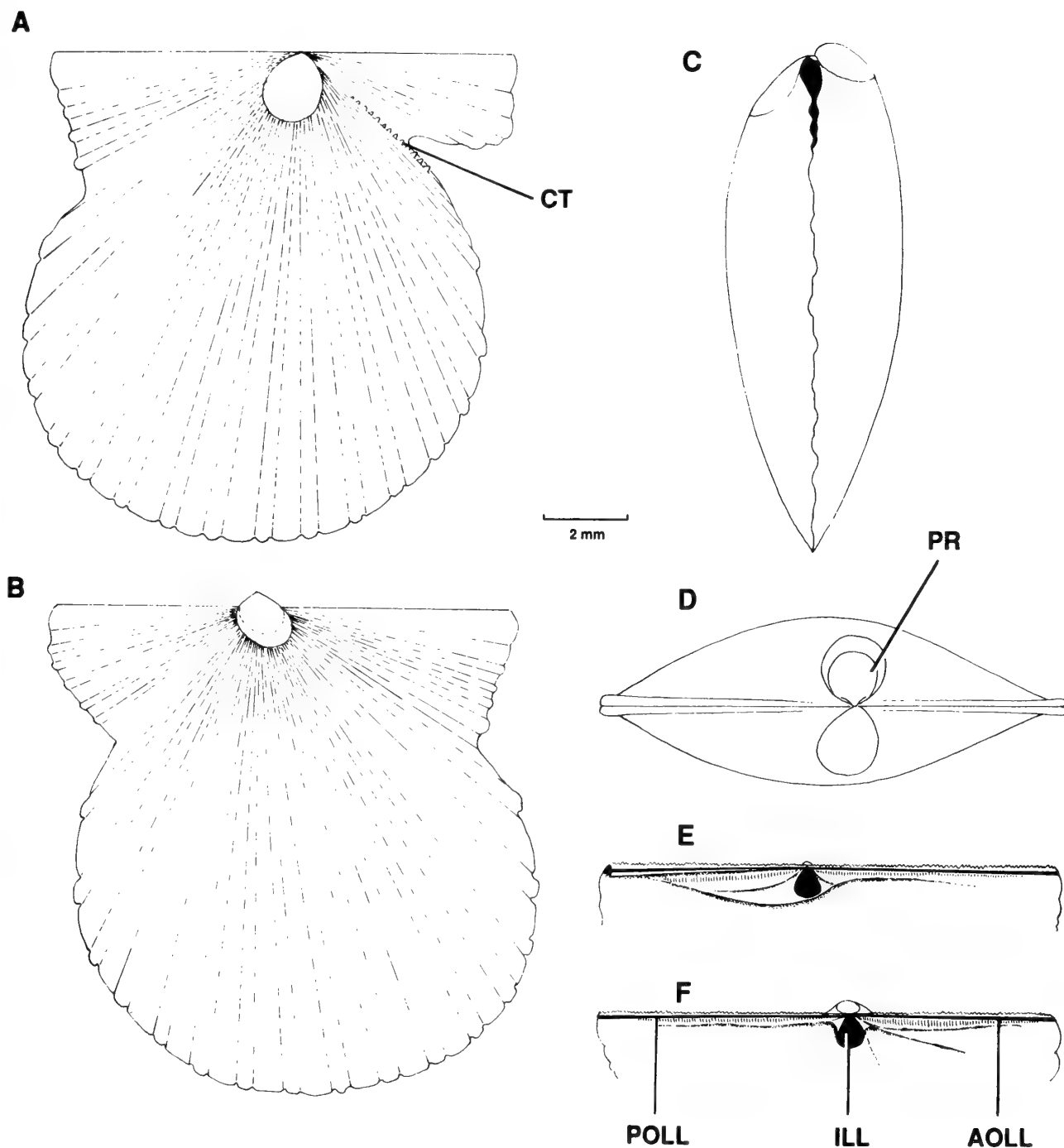


Figure 3

Leptopecten latiauratus. The shell as seen from A, the right; B, the left; C, the anterior and D, the dorsal aspects. E, an internal view of the hinge of the right valve; F, the left valve.

two components; a larger block of striated or "quick" fibers (PA(Q)) is thought to be responsible for rapid, phasic adduction of the shell valves. Encircling the postero-ventral edge of the "quick" component is the smaller "slow" component of smooth muscles (PA(S)). As in other scallops,

the orientation of these muscle blocks and the positions and sizes of the insertions upon left and right valves are different, but not so different as in *Amusium* and *Propeamussium* (Morton, 1980; Morton & Thurston, 1989), which are good swimmers.

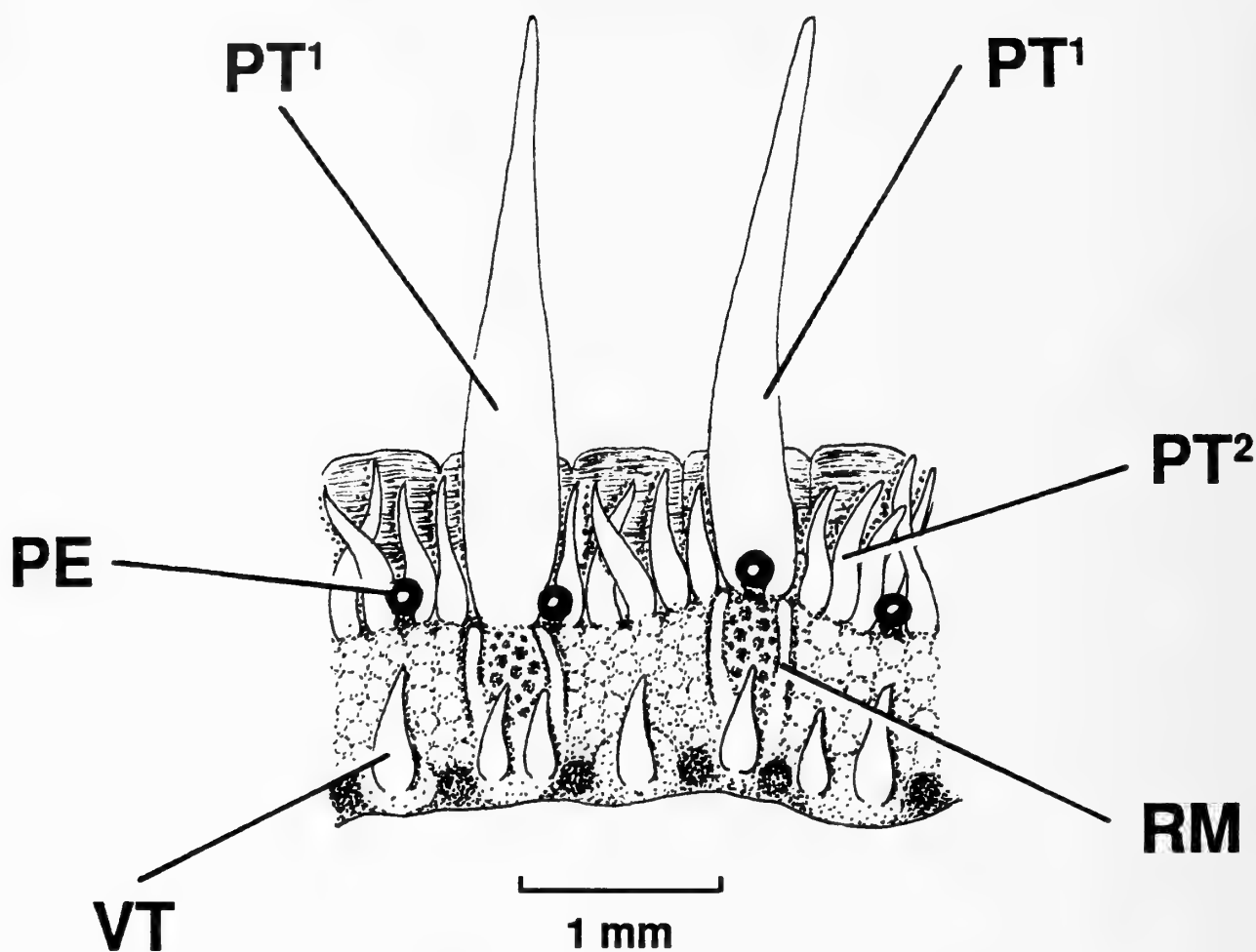


Figure 4

Leptopecten latiauratus. A detailed view of the mantle margin.

The significance of muscle obliquity in the Pectinoidea has been discussed by Thayer (1972) and Morton (1980); it assists, for example, in pressing the dorsal margin of the right valve against that of the left, preventing shear, in conjunction with the interlocked ventral shell margin.

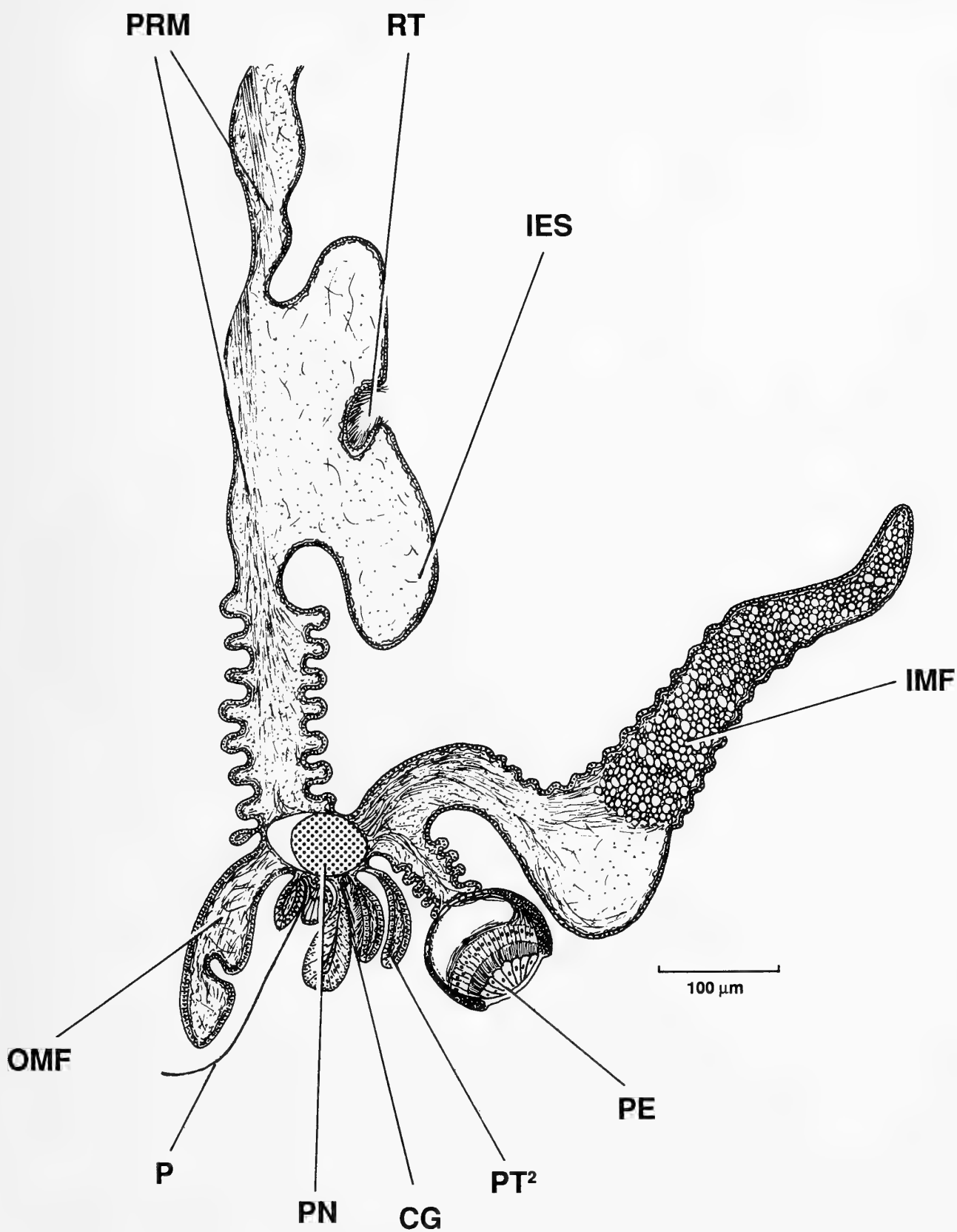
There is a single, left, pedal retractor muscle (LPRM), which is inserted on the left shell valve just dorsal to the adductor muscle. Such a situation is typical of other pectinids, but not propeamussids, which have lost all pedal retractor muscles (Morton & Thurston, 1989).

The mantle: The mantle margin is illustrated in Figure 4 and shows the middle fold with primary (PT¹) and secondary (PT²) tentacles and pallial eyes. The inner fold forms a velum which also possesses velar tentacles. (VT). Paired retractor muscles (RM) serve to retract the velum, differentially, along its length. The velum is pale yellow with pigmented brown marks marginally, between each velar tentacle. Between pairs of retractor muscles, the mantle is darker. In transverse section (Figure 5), the general

mantle under the shell is thin, the two epithelia of simple construction, although the space between them (IES) is a capacious haemocoel. The mantle margin is of the typical pectinid plan (Dakin, 1909; Morton, 1980) and comprises the usual three folds (Yonge, 1982). The outer fold (OMF) secretes the shell from its outer surface, the thin perios-tracum (P) from its inner. The middle fold lies between the outer and the inner folds (IMF) and bears on its inner surface the primary (PT¹) and secondary tentacles (PT²) plus pallial eyes (PE) which are located at the base of the inner fold. The inner fold (IMF) is in the form of a muscularized velum which is not, however, of the same enormous dimensions as that of *Propeamussium lucidum*

Figure 5

Leptopecten latiauratus. A transverse section through the right mantle margin.



(Morton & Thurston, 1989) and possesses tentacles (VT) on its outer surface.

The pallial eyes are of the same configuration as those of *Pecten* and *Amusium* (Dakin, 1909, 1928; Morton, 1980) and comprise a cellular lens overlain by a cornea and surrounded by a tapetum. There is a ciliary-based retina. As will be described, the inner surface of the mantle possesses ciliated rejectory tracts, the ventral one of which is illustrated in Figure 5 (RT). Another ciliary groove (CG) occurs on the outer surface of the middle mantle fold and presumably keeps the outer surface of the mantle clean. There is a relatively large pallial retractor muscle (PRM) and a large pallial nerve (PN).

The posterior pallial gland and abdominal sense organ:

On each mantle lobe, postero-ventral to the "slow" component of the posterior adductor muscle, occurs a large, tan-colored gland, which is raised above the general mantle surface (Figures 7, 8, 11, PPG).

In section (Figure 6A), the gland has a structure which is similar to that described by Morton (1982b) for *Bath-yarca pectuncoloides*. The outer mantle epithelium comprises simple squamous cells. Between this and the inner glandular epithelium (PPG) are located bundles of the pallial retractor muscle (PRM) and a wide inter-epithelial space (IES), the two epithelia being occasionally cross-connected by fine muscle fibers. In more detail (Figure 6B) the gland comprises two cell types; one is a tall (60 μm) secretory cell with a light staining epithelium (SEC). These are interspersed apically by inversely conical "supporting" cells (SUC) which possess intracellular pigment granules (and which presumably give the gland its color); from their apical surfaces also arises the occasional cilium. Such cilia are not, however, powerful, and pseudofeces are not swept across the gland by them, although particles in suspension in the outflowing water are.

Oliver & Allen (1980) described the gland as a "mantle flap gland" in the arcoideans discussed by them and suggested that it produces mucus which helps to bind up and thus aid in the removal of particulate wastes.

Abdominal sense organs have been described for many Pteriomorphia (Haszprunar, 1983), e.g., members of the Dimyidae (Yonge, 1978) and for *Pecten maximus* and *Placopecten magellanicus* by Dakin (1909) and Moir (1977), respectively. In *Leptopecten latiauratus*, a single abdominal sense organ occurs on the right side of the body and is located between the postero-ventral edge of the anterior adductor muscle, close to the rectum, and the antero-dorsal edge of the right posterior pallial gland (Figure 6A, ASO). In section (Figure 6C), it comprises a flap of tissue, the apex of which is swollen to form a dome-shaped cap. The cells of the cap are tall (up to 60 μm), and from their distal margins arises a mass of long (20 μm) cilia (C). The cells appear multinucleate, but Dakin (1909) suggested, for the same organ in *Pecten maximus*, that many of these nuclei may be those of nerve cells which form a network amongst the ciliated epithelial cells. Such nerve fibrils (NF) can also be seen in sections of this organ in *L. latiauratus*. The

nerve fibrils join up at the base of the abdominal sense organ to form a nerve (NVG) that connects with the visceral ganglia.

The close proximity and presumed nervous connection of the posterior pallial gland and abdominal sense organ in *Leptopecten latiauratus* and, in other pteriomorphs, suggest that they function synergistically. The abdominal sense organ may detect rates of flow and possibly, particle load in the exhalant stream, the posterior pallial gland functioning to bind up such material in mucus. No function has been definitively attributed to the abdominal sense organ, although it possesses both the positional and structural criteria necessary for it to function as a receptor (Moir, 1977).

The ciliary currents of the mantle: The ciliary currents of the mantle of *Leptopecten latiauratus* are shown in Figure 7. Essentially, water can enter the mantle cavity at any point antero-ventrally, and ciliary currents on the mantle internal to the marginal lobes reflect this. Mid antero-ventrally, however, a distinct tract, within which particles accumulate, passes dorsally and bifurcates at a point just beneath the position of the outer labial palp. A dorsal component receives input of material from the dorsal regions of the mantle cavity and transports it in a posterior direction, under the posterior adductor muscle and beneath the posterior pallial gland to be discharged as pseudofeces from the posterior exhalant aperture. A second rejection tract passes postero-ventrally from the point of bifurcation and receives input from the ventral regions of the mantle cavity. Material travelling in this rejection tract is eventually also expelled from the mantle cavity at the posterior exhalant aperture, along with material from the dorsal tract.

The ctenidia: The ctenidia of *Leptopecten latiauratus* (Figure 8), comprising inner (ID) and outer demibranchs (OD), are large and curve around the posterior adductor muscle from the anterior to the posterior, anteriorly attached to the visceral mass and mantle by suspensory membranes, but posteriorly free to project into the exhalant aperture.

The ctenidia of representatives of the Pectinidae have been studied by Ridewood (1903), Atkins (1936), Owen & McCrae (1976) and Yonge (1981). *Leptopecten latiauratus* is a pseudolamellibranch of conventional form i.e., the ctenidia have a gill ciliation of type B(1b) (Atkins, 1937), with acceptance tracts located in the ctenidial axis, on the ventral margins of both demibranchs, and in the junctions of the ascending lamellae of the inner and outer demibranchs with the visceral mass and mantle, respectively.

The ctenidia are plicate, each plica comprising, on average, eight filaments. As in other pseudolamellibranchs, the ciliary currents on the principal filaments beat upwards; those on the ordinary filaments beat downwards. Dorsal and ventral orally-directed acceptance tracts are thus generally served by different filaments.

The labial palps and mouth: The ctenidial-labial palp junction (Figure 9) is of Category 3 (Stasek, 1963) in that a few of the anterior filaments of both demibranchs project

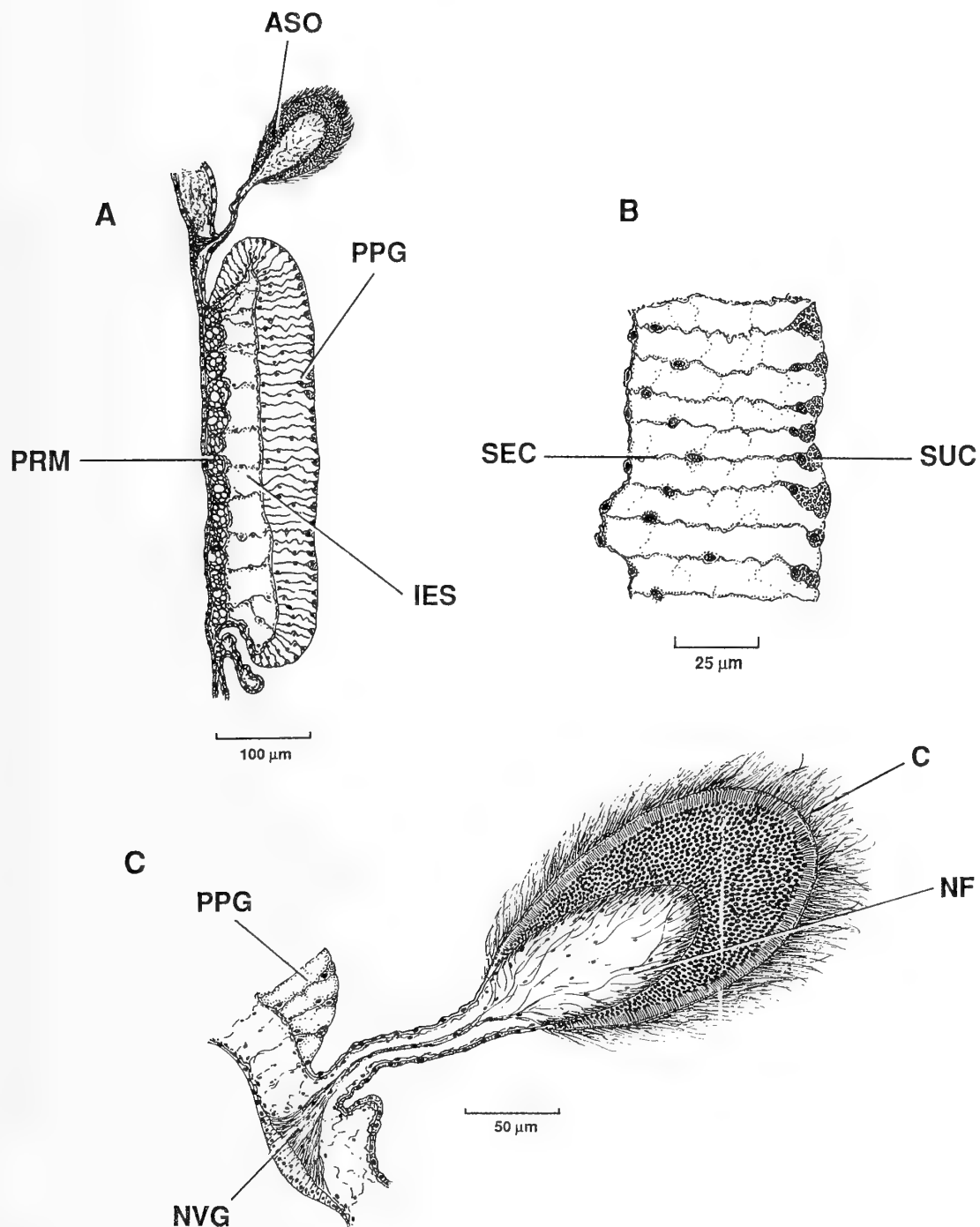


Figure 6

Leptopecten latiauratus. A, A section through the posterior pallial organ and abdominal sense organ of the right mantle lobe. The two organs are illustrated in greater detail in B and C, respectively.

directly between the labial palps. The labial palps are relatively large and possess only a few sorting ridges and grooves. Generally, cilia on the crests of the ridges beat toward the mouth, but a more detailed picture (Figure 10) shows the other sorting and rejection currents.

On the crests of each ridge, weak cilia transport particles toward the palp margins (I). On the aboral side of the apex of each ridge, cilia beat outward from the groove (II), although on the oral surface, they beat into the groove (IX). On oral and aboral sides of each ridge, cilia beat

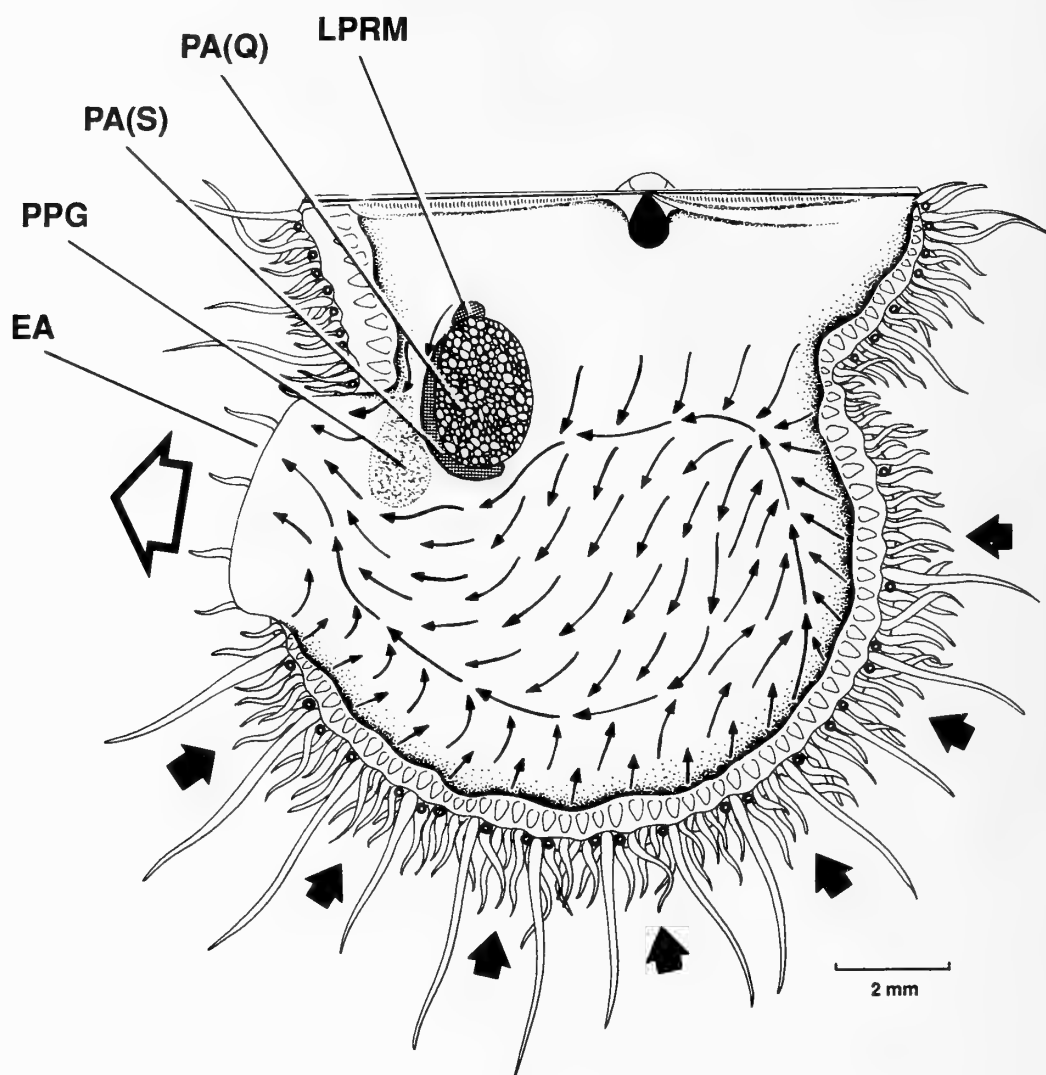


Figure 7

Leptopecten latiauratus. The ciliary currents of the mantle of the left side.

particles toward the palp margins (III; VIII); although, on the aboral surface, they also pass material into the groove (IV). In the depths of the groove, cilia beat downward on the oral face (VII) but toward the palp margins on the aboral face (V), as in the bottom of the groove (VI). The various ciliary currents of the labial palps therefore fulfill a sorting role with, ultimately, acceptance or rejection of particles for ingestion. The strength of the rejectory currents, however, suggests strongly that *Leptopecten latiauratus* has to deal with large quantities of particulate material entering the mantle cavity and being filtered by the ctenidia. The palps must thus remove much of this material for eventual expulsion at the exhalant aperture.

The lips of the mouth are foliose as is typical of the monomyarian Limoidea and Pectinoidea (Dakin, 1909; Gilmour, 1964, 1974; Bernard, 1972; Morton, 1979). The

foliose, unfused nature of the lip margins makes them of Type B (Morton, 1979). Inner and outer lips interdigitate such that they form a roof over the mouth and oral grooves, as in *Pecten maximus* and *Lima lima* (Dakin, 1909; Bernard, 1972; Morton, 1979).

The visceral mass and foot: The visceral mass is located antero-ventrally to the posterior adductor muscle (Figure 11). It extends dorsally to fill the sub-umbonal spaces of the left valve, particularly, with the stomach and surrounding digestive diverticula (DD). From the anterior edge of the visceral mass arises a long, thin foot with a swollen tip, which can be extended far beyond the anterior margin of the shell. There is a byssal gland which secretes a substantial byssus (Figure 8, BG). The visceral mass medially contains the testis; ventrally, the ovary. Histological

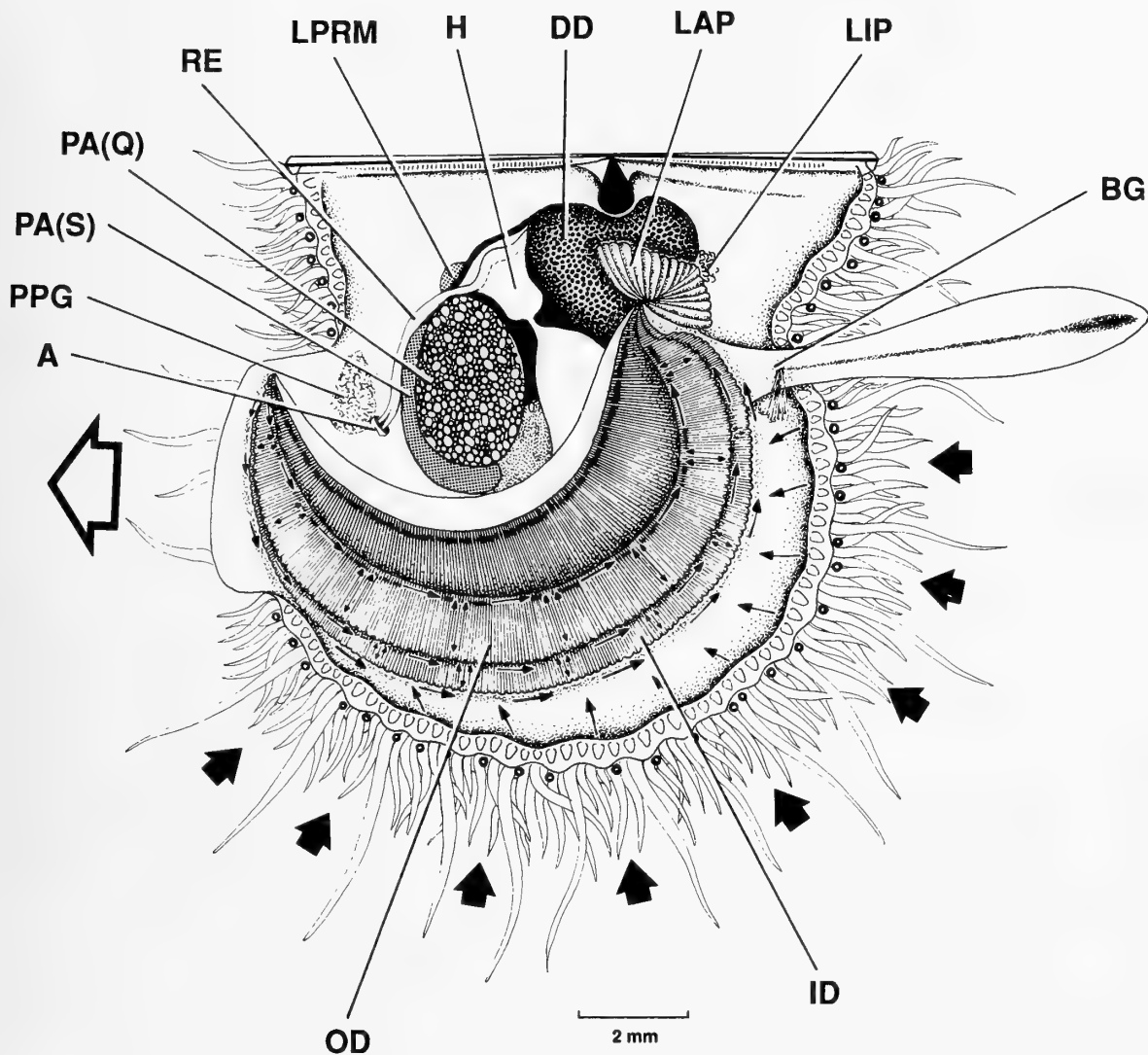


Figure 8

Leptopecten latiauratus. The organs and ciliary currents of the mantle cavity as seen from the right side after removal of the right shell valve and mantle lobe.

examination of the different sized individuals of *Leptopecten latiauratus* shows that all are simultaneous hermaphrodites, and although both sexes were at the same stage of maturity, it is unknown if there is simultaneous release of eggs and sperm, and thus, if self-fertilization is possible.

The ciliary currents of the visceral mass: The ciliary currents of the visceral mass are illustrated in Figure 11. Dorsal regions of the visceral mass, lateral to the testis (TE), possess cilia which beat downwards. From a point on the antero-ventral edge of the visceral mass, particles of material are passed upwards and are recirculated downwards at a point just below the position of the edge of the outer margin of the inner labial palp. All particles of

material, however, eventually join a generalized flow posteriorly along the medial axis of the visceral mass to pass under the anterior adductor muscle (PA(Q); PA(S)), and terminate on the pointed posterior edge of the visceral mass from which they are either wafted out of the exhalant aperture by the exhalant flow or fall onto the similarly rejectory currents of the mantle and are similarly expelled. The ciliary currents of the visceral mass thus complement those of the mantle.

Statocysts: The statocysts of *Leptopecten latiauratus* (Figure 12) are located inequilaterally above the pedal ganglia (PG) in the dorsal region of the visceral mass at the base of the foot and byssus gland.

The left statocyst (LS) is larger than the right (RS), the

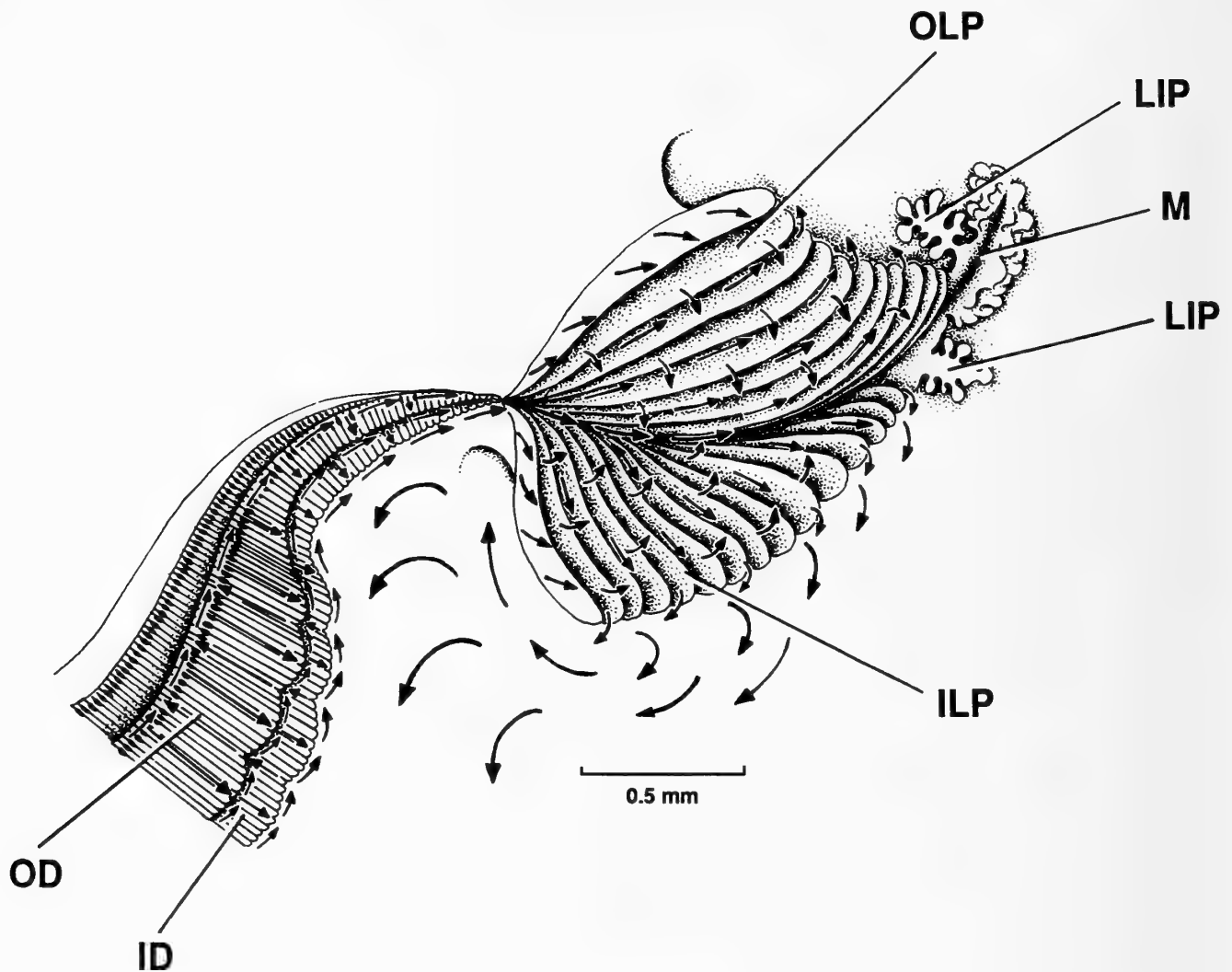


Figure 9

Leptopecten latiauratus. A detail of the ctenidial labial palp junction of the right side.

former some 80 μm in diameter, the latter some 60 μm . Such a situation is typical of the Pectinidae (Buddenbrock, 1915). Each statocyst comprises a capsule (CA) internal to which is an epithelium that comprises two cell types: a narrow, non-ciliated supporting cell (SUC) with a round nucleus 3 μm in diameter and a hemispherical ciliated sensory cell (SEN) with a kidney-shaped nucleus some 6 μm in diameter. From the apex of each of these latter cells arises a bunch of ~ 3 cilia some 10 μm long. The lumen of each statocyst is occupied by a mass of crystalline statocornia. The statocysts conform to type B₃ of Morton (1985), in that there is no regularly shaped major statolith.

Barber & Dilly (1969) described the statocyst of *Pecten maximus* as comprising two cell types, i.e., ciliated sense cells and supporting cells, as described here for *Leptopecten*

latiauratus. Cragg & Nott (1977), however, suggested that the cells were only of one type. The different size and shape of the nuclei of the two cell types here described for *L. latiauratus* suggest two cell types.

The alimentary canal: The course of the alimentary canal in the visceral mass is illustrated in Figure 11. An esophagus opens into the anterior end of the stomach. The conjoined style sac and mid gut (CSMG) arise from the postero-ventral floor of the stomach. The style sac is short and the mid gut (MG) separates from it in the ventral visceral mass to turn upwards and penetrate the ventricle of the heart (H) as the rectum (RE), pass over the quick component of the posterior adductor muscle (PA(Q)) and terminate on the posterior face of the slow component of

the adductor muscle (PA(S)) as an anal papilla (A) that is free of attachments.

The stomach of *Leptopecten latiauratus* is of Type IV (Purchon, 1957) and closely similar to that of *Pecten maximus* (Graham, 1949), *Spondylus hystrix* (Purchon, 1957), but not *Propeamussium lucidum* (Morton & Thurston, 1989), the latter being simplified for a carnivorous diet. The stomach of *L. latiauratus* lies dorsally in the visceral mass and when examined from the right side (Figure 13) has the following internal architecture.

From the opening of the style sac, which is conjoined with the mid gut (CSMG), arises a crystalline style (CS) that rotates against a postero-dorsal gastric shield (GS). Also from the conjoined style sac and mid gut arises the minor typhlosole (MT), which terminates quickly on the right wall of the stomach, and the major typhlosole (T) which sweeps across the floor of the stomach to pass in front of the food sorting caecum (FC) and terminates near the opening to the left pouch (LP). The entrance to the left pouch receives a spur from the gastric shield and from it arise two major openings to the digestive diverticula of the left side. A sorting area (SA⁴) lines the anterior edge of the gastric shield and connects the left pouch with the dorsal hood (DH). The intestinal groove (IG), which accompanies the major typhlosole, receives unselected particles of potential food material entering the stomach and transfers them to the mid gut for eventual defecation. The food sorting caecum possesses a sorting area (SA) that directs particles either upwards and into the food sorting caecum or outwards to its margin and so into the general stomach. A larger sorting area (SA) lies on the right side of the stomach and similarly directs particles either into the intestinal groove or into a duct of the digestive diverticula (DDD¹) under the opening from the esophagus (O). On the right side of the stomach are the openings of three ducts which lead to the digestive diverticula of the right side (DDD²⁻⁴). A ciliated ridge (R) on the dorsal surface of the stomach leads into the dorsal hood and into which it carries particles of potential food.

The stomach architecture of *Leptopecten latiauratus* thus suggests the sorting, selection, digestion, and absorption of fine particles of food.

The organs of the pericardium: The pericardium of *Leptopecten latiauratus* (Figure 14) lies dorsally between the digestive diverticula (DD) of the visceral mass and the posterior adductor muscle (PA(Q)). It contains a heart which comprises a central ventricle (V), penetrated by the rectum (RE) and lateral auricles (AU). The kidneys lie beneath the posterior adductor muscle and the reno-pericardial apertures (RPA) are thus situated on the postero-ventral edge of the pericardium. Each reno-pericardial aperture leads into a distal, bag-like kidney limb (DK). These enclose and open into the much narrower proximal kidney limbs (PK). Each proximal limb discharges into the supra-branchial chamber on the visceral mass at a renal

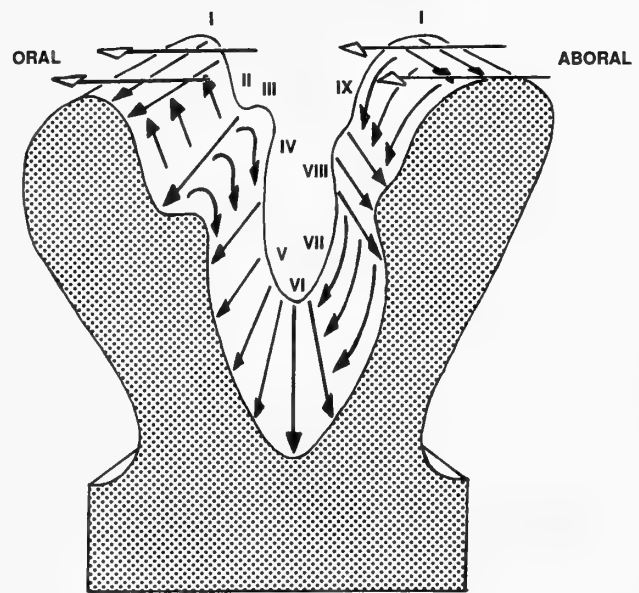


Figure 10

Leptopecten latiauratus. The ciliary currents of two ridges and a contained groove of the labial palps. (For explanation see pp. 12–14).

aperture (RA). The single gonopore (G), receiving gametes from both the testis (TE) and the ovary (OV), is located antero-ventral to the renal aperture. The pericardial gland is colorless and lines the pericardial wall.

DISCUSSION

Leptopecten latiauratus has a geographic range from Point Reyes, California (38°N), to Cape San Lucas, Baja California, Mexico, and north to Espiritu Santo Island in the Gulf of California and Guadalupe Island, Mexico (Grau, 1959; Bernard et al., 1991). Grau (1959) also recorded it as having a depth range of from just below low tide to 125 fathoms (229 m), and attaching to either rocks or pilings in shallow water. In deeper waters, it attaches to rocks on shale, gravel, and sand bottoms and to calcareous algae. The individuals presently reported upon were attached to every kind of substratum, i.e., stones, discarded netting, empty shells, gorgonians and plastic rubbish. Morris et al. (1980) described a similar depth range and equally diverse substrate preferences for this species.

Grau (1959) reported that two subspecies of *Leptopecten latiauratus* i.e., *L. l. latiauratus* and *L. l. monotimeris*, occur in southern California. Formerly considered discrete species (McLean, 1978), these subspecies are now adjudged to be ecomorphs, the former occurring on rocks and pilings, the latter on rocks, kelp (*Pelagophycus* and *Macrocystis*) in open water, and *Zostera* in bays. Water temperature is reported to be strongly influential upon shell morphology (Clark, 1971). *L. latiauratus* is a well-known fouler of

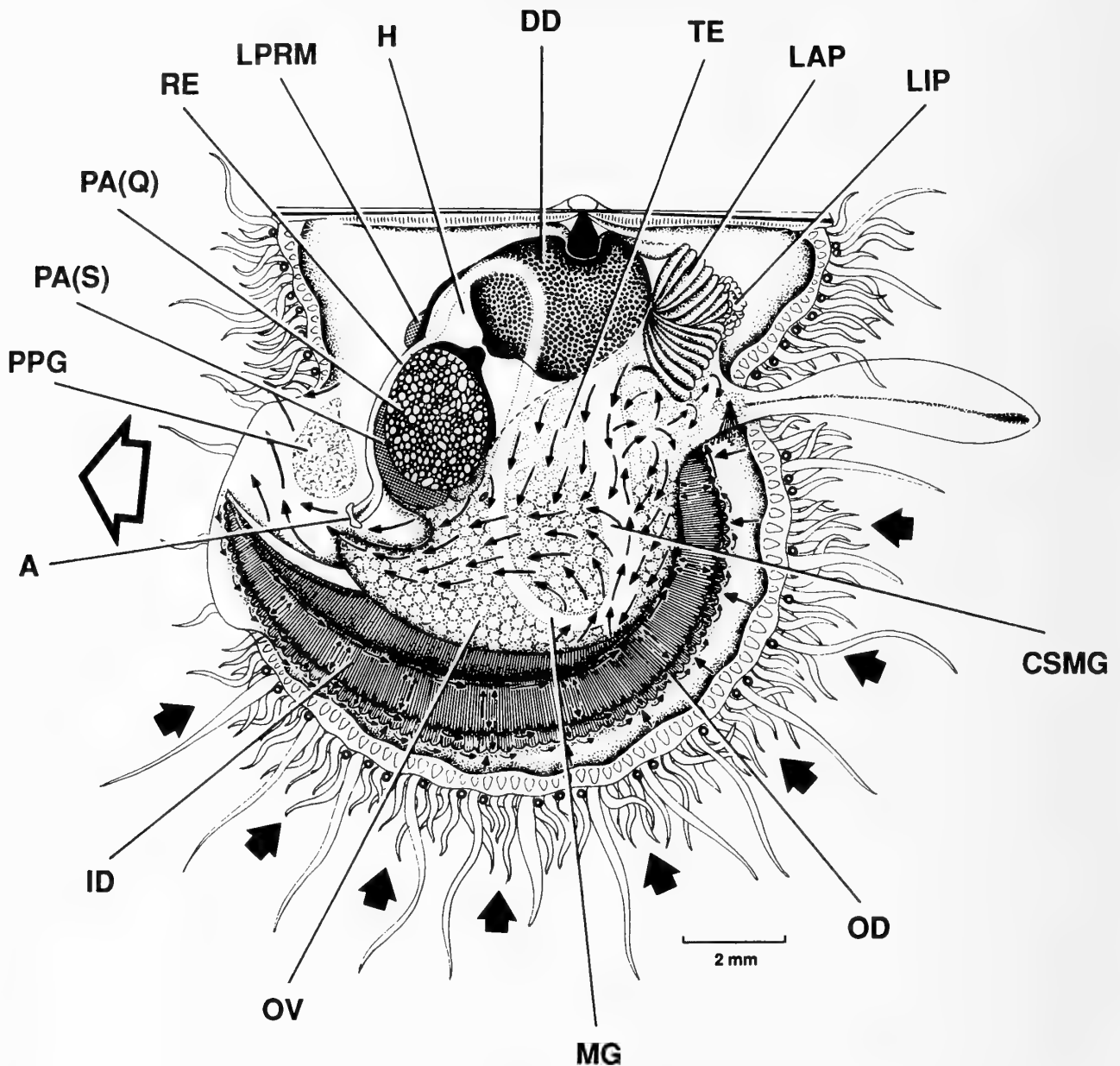


Figure 11

Leptopecten latiauratus. The organs and ciliary currents of the mantle cavity as seen from the right side after removal of the right shell valve and mantle lobe and right ctenidium. The course of the gut in the visceral mass is also indicated.

pilings and experimental test blocks placed in the waters off southern California (Coe, 1932) and has strong powers of locomotion, typically upwards (Clark, 1971). Coe (1932) showed that young individuals (1.5–2 mm in greatest diameter) appeared on his test blocks from July–October, while mature individuals were recorded from May to August. Clark (1971) recorded that 12 of 15 individuals of *L. latiauratus* established in an aquarium doubled in size

over a period of ~5 weeks. Coe (1932) similarly recorded fast rates of growth for this species and suggested an annual cycle of reproduction, with sexual maturity occurring at an age of between 9–12 months at a shell height of between 25–28 mm.

McPeak & Glantz (1982) recorded a massive settlement of *Leptopecten monotimeris*, the “Kelp scallop” ecomorph of *L. latiauratus* (the “Broad-eared *Pecten*” of Morris et

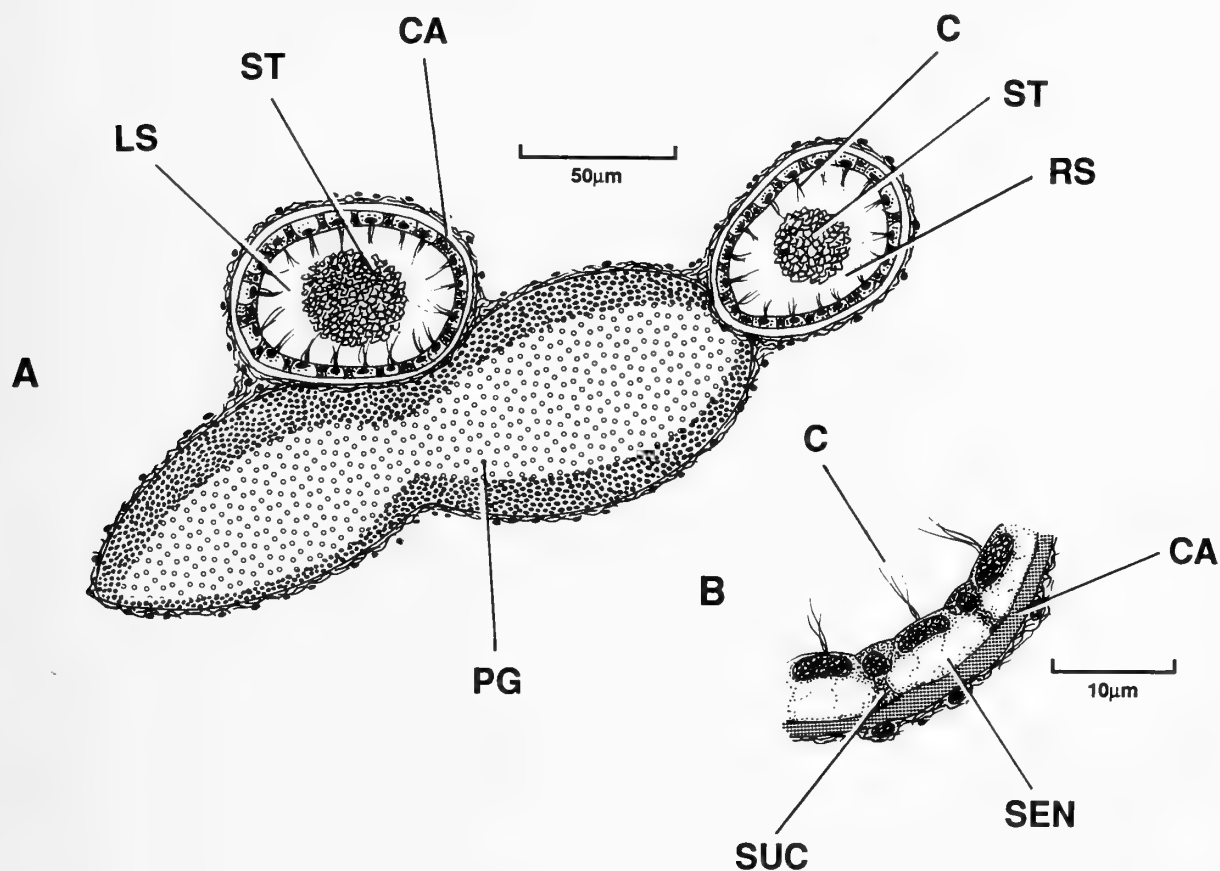


Figure 12

Leptopecten latiauratus. A, A transverse section through the pedal ganglia and left and right statocysts; B, a detail of the statocyst epithelium.

al. (1980)), upon *Macrocystis* growing on the Standard Oil platform "Hazel" in 1958, one month after the platform was established (Carlisle et al., 1964). After one year, however, the scallops had been displaced by the blue mussel, *Mytilus edulis*. Notwithstanding, the scallops were reported by McPeak & Glantz (1982) to be in spawning condition throughout the year and individuals of <1 mm in shell height were observed almost every month. Mature individuals were recorded within six months of settlement.

Dense settlement of *Leptopecten latiauratus* also occurred on oil platform "Hilda" in 1960, but with blue mussels again replacing them by 1961 (Turner et al., 1969). These authors also recorded large settlements of this species upon oil platforms in 1958 and 1959. McPeak & Glantz (1982) reported massive settlement of *L. latiauratus* upon an artificial reef, the San Diego-La Jolla Underwater Park Reef, soon after it was constructed in 1975. The same authors recorded a massive settlement of *L. latiauratus* on *Macrocystis* kelp at Point Loma, California, in 1977. Their observations confirm those of others, e.g., Limbaugh (1955), Clendenning (1960) and Carlisle et al., (1964) that set-

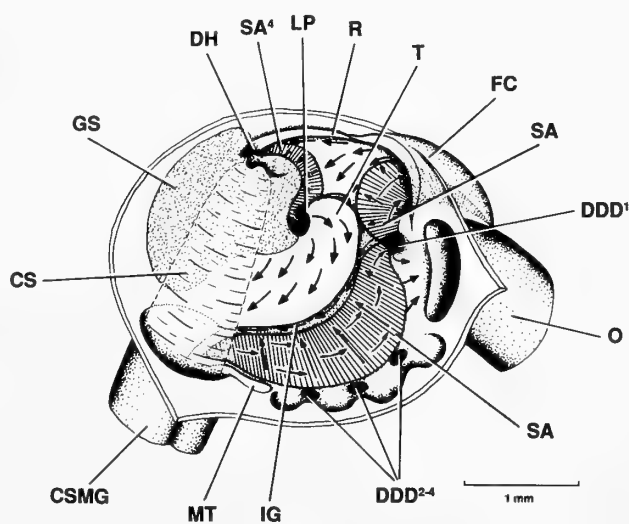


Figure 13

Leptopecten latiauratus. The structure and ciliary currents of the stomach as seen from the right side.

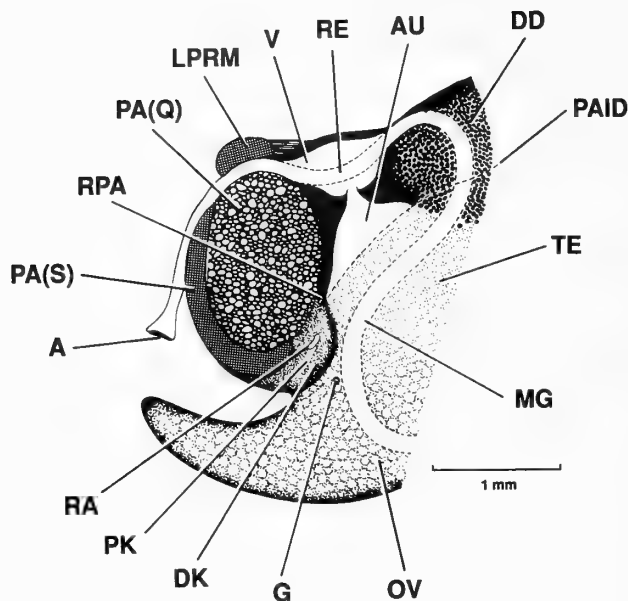


Figure 14

Leptopecten latiauratus. The organs of the pericardium as seen from the right side.

tlement of *L. latiauratus* can be so prolific as to result in sinkage of the kelp and its subsequent death.

Leptopecten latiauratus is a simultaneous hermaphrodite. Coe (1932) suggested that the species breeds once each year, from May to August and that individuals mature at a maximum shell dimension of between 25 and 28 mm. This study, however, suggests that individuals of approximately 5.5 mm shell height are sexually mature, such individuals also corresponding with a greater incidence of empty valves in the samples obtained. Somewhat larger individuals (7.5–8.5 mm) were spent. Yet larger individuals (8.5–12.5 mm) were either maturing or mature, this coinciding with a peak of living individuals in the sample. An interpretation of the above picture suggests that *Leptopecten latiauratus* reproduces once a year (Coe, 1932) and that juveniles mature quickly, within one year, and suffer early mortality following spawning. Surviving individuals enter a second year of life and mature once again. On artificial substrates, however, Carlisle et al. (1964) recorded that *L. latiauratus* has year round reproductive abilities, larvae apparently occurring in the water column also year round (Turner et al., 1969).

Morton (1991) has suggested for a spectrum of Hong Kong bivalves that individual species fit into the broad categories of *K* and *r*-selected (Pianka, 1970). One of those assessed to be an *r*-strategist is *Corbicula fluminea*, an opportunistic colonizer of fresh waters that has been introduced elsewhere, including the U.S.A., from its Asian range. *C. fluminea* is a short-lived, polymorphic, hermaphrodite. The analogy with *Leptopecten latiauratus*, which is also a

short-lived, polymorphic, hermaphrodite that colonizes newly-available marine substrates, is compelling.

Leptopecten latiauratus is byssally attached and can swim only weakly when detached, making one or two adductions that lift it briefly from the substratum. Thus, colonization of newly available substrates is by often massive, juvenile recruitment (McPeak & Glantz, 1982). Detached individuals can and do, however, actively locomote using the well-developed foot as is typical of many such scallops (Waller, 1976). A newly available substrate can thus be explored, following juvenile recruitment. Gregarious settlement on a newly available substratum enhances the chances of cross-fertilization (even though the species is a simultaneous hermaphrodite), thereby promoting genetic exchange. Gregarious settlement also implies synchronized spawning and thus, a finely tuned stimulus. Such a self-reinforcing reproductive strategy, in addition to information on the life history, supports the suggestion made here, therefore, that *Leptopecten latiauratus* is an opportunistic *r*-strategist.

Such a life history strategy seems to be in direct contrast to that characteristic of larger, commercially important, and often abyssate species of continental shelf species, e.g., *Placopecten magellanicus* (Dickie, 1955) and *Amusium pleuronectes* (Morton, 1980). The cryptic *Hinnites multirugosus* was deemed by Yonge (1951) to be dioecious. There seems, therefore, to be among the Pectinoidea the possibility of an *r-K* continuum, and it would perhaps be instructive for this genus- and species-rich superfamily to be evaluated in the context of the spectrum of life history strategies and sexual tactics adopted.

In terms of its anatomy, *Leptopecten latiauratus* is not unlike other scallops, except with regard to species of *Propeamussium*, which is a genus of deep-water, swimming, predatory scallops of remarkably ancient ancestry (Waller, 1971). In these bivalves, the basic scallop anatomy is adapted for the capture of living prey with non-filtering ctenidia, non-sorting labial palps, a muscular mouth and simplified stomach architecture (Morton & Thurston, 1989). The anatomical features of *Leptopecten latiauratus* are all for filter feeding with large, filtering ctenidia, sorting labial palps, and interdigitating folds to the lips of the mouth. These help prevent food from being flushed out of the oral grooves during phasic adduction and are of the simplest type identified (Morton, 1985), characteristic of byssally attached, non-swimming limids and pectinids. The ciliary currents of the mantle cavity are powerful, particularly of the mantle and visceral mass which are concerned with rejection of pseudofeces. Though sometimes attaching to kelps in shallow water, *Leptopecten latiauratus* must attach naturally, in deeper waters, to any solid object on the sea bed where fine silts are abundant. Strong cleansing currents are therefore essential, there even being ciliary tracts on the outer surface of the middle mantle fold. Strong ciliary rejection tracts are also characteristic of *Pecten maximus*, but not the cryptic *Hinnites multirugosus* occupying water with little sediment (Yonge, 1951).

In conclusion, therefore, *Leptopecten latiauratus* is a short-lived, opportunistic, scallop of shallow and deeper cold waters off the coast of California. It has the basic scallop plan to deal with a sediment laden inhalant stream and is byssally attached, but with strong powers of pedal, but not swimming, locomotion for relocation following initial gregarious settlement.

ACKNOWLEDGMENTS

I am grateful to Paul H. Scott (Santa Barbara Museum of Natural History) and Gene Coan for organizing this research opportunity following the 1991 meeting of the American Malacological Union and to the latter for providing some of the local literature references to *Leptopecten latiauratus*. The Director, Dr. James Nybbaken, and the staff of the Moss Landing Marine Laboratories are thanked for providing bench and boat facilities for this work. Mr. H. C. Leung (The University of Hong Kong) is thanked for histological assistance. Dr. T. R. Waller (United States National Museum, Washington, D.C.) is thanked for his critical reading of the first draft of the manuscript of this paper.

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International Workshop on the Marine Bivalvia of California

The Functional Morphology and Biology of
Pandora filosa (Carpenter, 1864)
(Bivalvia: Anomalodesmata: Pandoracea)

by

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Abstract. In terms of shell form, internal anatomy, and burrowing behavior, *Pandora filosa* is similar to other members of the genus. Hinge dentition varies interspecifically being like that of eastern but unlike that of western Atlantic species. A rotation of the lyonsiid-like ligament seen in some larger species of *Pandora* is lacking and can be correlated with less lateral compression. The burrowing behavior of *P. filosa* indicates that it is usually oriented either upon or within the substrate, with the convex left valve down.

INTRODUCTION

Members of the Anomalodesmata Dall, 1899, are noteworthy because of their phylogenetic age (Paleozoic) and the high degree of specialization that many species exhibit (Morton, 1984). This subclass contains the sole order Pholadomyoida Newell, 1965, though others argue that the septibranchs belong in a separate order (see Morton, 1985). The Pholadomyoida is divided into eight superfamilies, which are further subdivided into nine extinct and 13 extant families (Morton, 1985). The evolutionary history of the Anomalodesmata has been reviewed by Runnegar (1974) and Morton (1985).

The Pandoridae Rafinesque, 1815, was considered to contain only the genus *Pandora* Bruguière, 1797, comprising five subgenera, i.e., *Pandora* s.s., *Pandorella* Conrad, 1863, *Heteroclidus* Dall, 1903, *Foveadens* Dall, 1915, and *Frenamya* Iredale, 1930 (Morton, 1984). Morton (1984) reviewed the literature on the Pandoridae and reestablished *Frenamya* as a valid genus.

Pandora first appeared in the Tertiary Period. It was absent in North America until the Miocene Epoch (Boss & Merrill, 1965). Numerous fossil species have been described worldwide. Recent *Pandora* tend to be boreal. Boss & Merrill (1965) reviewed the western Atlantic *Pandora* and showed the various species to be united by a variety of morphological features, i.e., pallial retractor muscles comprising individual muscle bundles, pedal retractor

muscles inserted to the adductor muscles, a reduced outer demibranch, a pedal aperture larger than in other Pandoracea and reduced dentiform processes on the hinge (Boss & Merrill, 1965).

Pandora is inequivalve, with a convex left valve and a flat right valve; both are fragile. Species composing the genus display varying degrees of lateral compression, which may increase with size. *Pandora* inhabits areas of sandy mud either burrowing or lying atop the substrate on either valve (Allen, 1954). The anatomy of Atlantic species, i.e., *Pandora inaequivalvis* (Linnaeus, 1758) and *Pandora pinna* (Montagu, 1803), was investigated by Allen (1954) and that of *Pandora gouldiana* Dall, 1886, by Boss & Merrill (1965). The gross anatomy and ciliary currents of the Pacific species *Pandora grandis* Dall, 1877, was described by Stasek (1963). Here, observations are presented on the Pacific species *Pandora filosa*, which occurs along the west coast of North America from Alaska to Ensenada Bay, California, at depths between 18 to 137 m (Abbott, 1974). The anatomy, ciliary currents of the mantle cavity, and burrowing behavior are described. Comparisons are made with congeners and other members of the Anomalodesmata.

MATERIALS AND METHODS

Seven live individuals of *P. filosa* were collected from Monterey Bay, California, in areas of sandy mud on 6 and 11

July 1991 near 36°49.7'N, 121°50.3'W and 36°50.2'N, 121°51.7'W, respectively, and at depths from 55 to 80 m. The material was collected aboard the Moss Landing Marine Laboratories research vessel R/V *Ricketts* using a small biology trawl. Animals were kept at the Moss Landing Marine Laboratories in an open circulating seawater system maintained at 15°C.

Burrowing experiments were performed over a period of 12 hours using sediment taken from Elkhorn Slough, Moss Landing, California. External morphology was examined, including that of the siphons. Individuals were then relaxed in 7% MgCl₂ and dissected. Ctenidial currents were observed using drawing ink diluted with seawater. Samples were fixed for 24 hours in a 5% formalin solution in seawater and subsequently stored in 70% ethanol. Sixteen specimens collected on 23 March 1988 and one specimen collected on 26 October 1991 by the staff of the Moss Landing Marine Laboratories from Monterey Bay were also examined. A 0.5% methylene blue staining solution was used during dissection of preserved animals to assist in the differentiation of various organ systems and structures.

The valves of 10 specimens of *P. gouldiana* taken from Long Island Sound and provided by Prof. R. C. Bullock of the University of Rhode Island, were also examined for comparative purposes. Voucher specimens of *P. filosa* have been deposited in the Division of Mollusks at the United States National Museum of Natural History, Washington, D.C., (Acc. No. 398250; Cat. Nos. USNM 860286, USNM 860287).

RESULTS

The Shell

Pandora filosa is inequivalve; the left valve is convex, the right flattened (Figure 1a, b). In closed individuals, the flattened right valve is pressed against and confined within the borders of the convex left valve (Figure 1b). This is permitted by the flexibility of the ventral margin of the right valve, as in species of *Propeamussium* (Morton & Thurston, 1989). The fragile valves are connected along the dorsal margin by the ligament and fused periostracum (FP) (Figure 1a, c). The largest individual examined measured approximately 15 mm in length, 7.5 mm in height and 4 mm in width, though the species can reach 25 mm in length (Abbott, 1974). The shell exterior is chalky white although the right valve (Figure 1e) has distinct radial lines (RL) that are frequently rust colored. Faint concentric growth lines characterize both valves. The left valve (Figure 1d) has a pronounced ridge (RI) leading diagonally from the umbo to the postero-ventral margin. The right valve also has a heavy ridge which begins at the umbo and extends along the dorsal margin. The posterior end is elongate in some larger individuals (Figure 1d) and covered by thicker, roughened periostracum (P) (Figure 1c, d).

The internal surface of both valves is smooth and na-

creous. Anterior and posterior adductor muscle scars are visible near the dorsal edge. The anterior adductor muscle scar is located halfway between the umbo and the anterior margin of the shell; the scar was 0.14 mm in diameter in a 15 mm long individual. The posterior adductor muscle scar occurs midway between the umbo and the posterior margin of the shell; it measured 0.18 mm in a 15 mm long individual. Anterior and posterior pedal retractor muscle scars occur ventral to the anterior and posterior adductor muscle scars, respectively. They are, however, almost indiscernible. Valves 10 to 15 mm in length have between five to seven rod-shaped pallial retractor muscle scars, distributed in the form of an arc between the adductor muscle scars, as in *P. gouldiana* (Boss & Merrill, 1965). The lengths of the pallial retractor muscle scars of the right valve become progressively greater posteriorly; in a 15 mm long individual, they increase in size from 0.02 mm to 0.18 mm. The pallial retractor muscle scar lengths of the left valve are more conservative and, in a 12 mm long individual, varied from 0.02 mm, anteriorly, to 0.05 mm, posteriorly. A slight depression begins at each pallial muscle scar and extends umbonally: a remnant of previous scars. Two wide parallel linear depressions occur at the posterior end of both valves; these provide the space in which the retracted siphons reside.

The internal opisthodetic ligament (Figure 2) resembles that of the Lyonsiidae (Yonge, 1976). It is composed of inner and outer layers with the central zone of the former calcified into a lithodesma (L). There is a small anterior outer ligament layer (AOLL) seen just anterior to the lithodesma, and the thin posterior outer ligament layer (not seen in Figure 2) covers the inner ligament layer (ILL). The ligament is attached to the valves by resilifers (RE). A secondary outer ligament is present in the form of fused periostracum (FP). The right valve has a hinge tooth (TH) which fits into a socket (S) in the left valve. This socket is defined by an anterior process (PR) and a small posterior tooth, located anterior to the anterior outer ligament layer.

The Siphons

The siphons (Figure 3) are surrounded at the base by approximately 15 tentacles ~1 mm in length; each tentacle extends beyond the siphonal openings and has one or two brownish pigment spots. The rim of the inhalant siphon (IS) is surrounded by six to eight tentacles, 0.25 mm in length, interspersed usually by one or two shorter tentacles, 0.10 mm in length. Tentacles of the inhalant siphon also contain small pigment spots. The tentacles can be moved backward or forward and may also be retracted to nearly half their length; all exhibit a slight iridescence. The exhalant siphon (ES) is cone-shaped, extends slightly beyond the inhalant and has a slight, dorsally directed curve.

When the siphons are withdrawn, the tentacles of the inhalant are brought together, first at their tips, then at their bases, thus closing the aperture. The lateral walls of the exhalant siphon are brought together medially; the

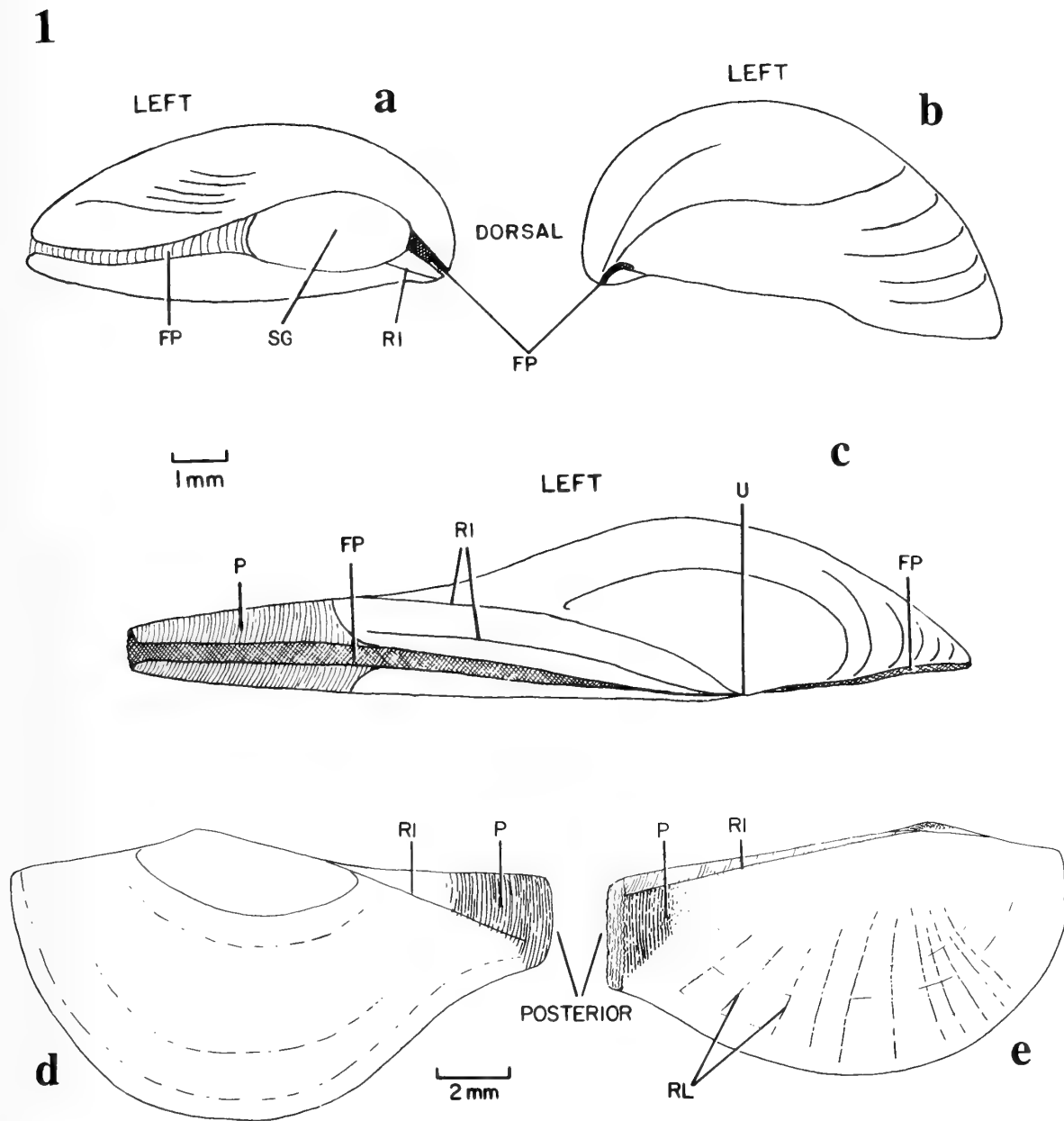


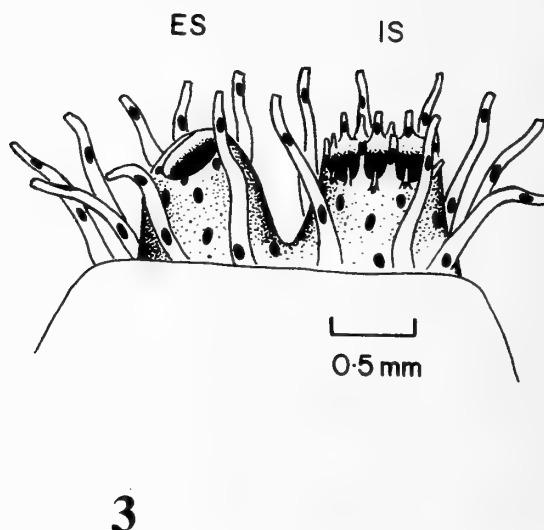
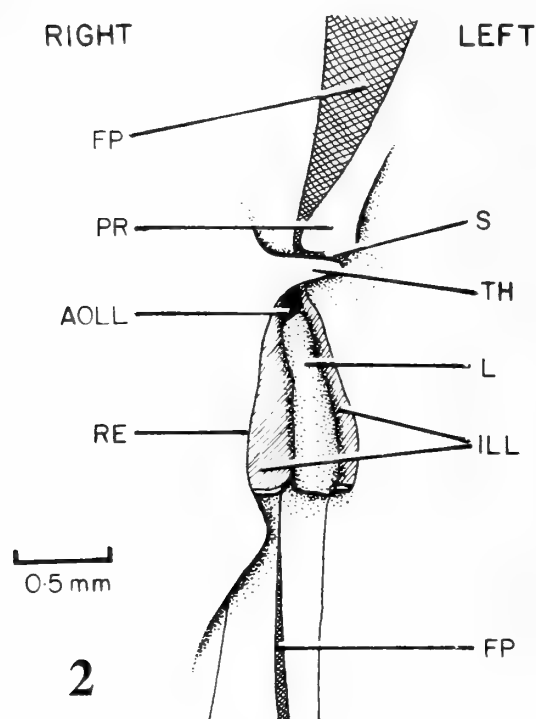
Figure 1

a. Posterior view, left and right valves. b. Anterior view, left valve and small portion of right valve. c. Dorsal view of valves showing the secondary ligament. d. External view of convex left valve. e. External view of flat right valve. 1 mm scale bar refers to a-c. 2 mm scale bar refers to d and e. Key: FP, fused periostracum; P, thicker periostracum; RI, ridge; RL, radial line; SG, siphonal gape; U, umbone.

siphonal margin then folding inward into the lumen, effectively closing the opening. Finally, a flap of sand-covered periostracum on the right valve covers the siphonal gape to camouflage the posterior end of the shell. The siphons are photosensitive as evidenced by their tendency to withdraw when a shadow is cast over them, i.e., there is a shadow reflex typical of the Bivalvia.

Organs of the Mantle Cavity

The muscular mantle is fused extensively along the ventral margin, except at the siphonal (ES & IS) and pedal gapes (PEGA) (Figure 4a, b). A fourth pallial aperture is lacking. The large foot (F) is laterally compressed, projects antero-ventrally, and has a ventral byssal groove. This



Explanation of Figures 2 and 3

Figure 2. Internal view of hinge showing primary and secondary ligament. Key: AOLL, anterior outer ligament layer; FP, fused periostracum; ILL, inner ligament layer; L, lithodesma; PR, process; RE, resilifer; S, socket; TH, tooth.

Figure 3. View of extended siphons as seen from the left side. Key: ES, exhalant siphon; IS, inhalant siphon.

groove begins in the distal region of the foot, continues posteriorly and ends as the foot widens. A triangular area exists at the posterior end of the byssal groove and extends dorsally to either side of the foot. It is seen only upon treatment with methylene blue. The foot possesses small anterior and posterior pedal retractor muscles.

The ctenidia are plicate and heterorhabdic, each plica having seven filaments. The inner demibranch (ID) is entire, whereas the outer demibranch (OD) is reduced and composed of descending lamellae only (Figure 4a). The plicae here are not readily apparent. On the outer demibranch, particles are carried ventrally onto the inner demibranch. The inner demibranch is comparatively large and comprises between 15 to 20 plicae. Particles are carried ventrally on both ascending and descending lamellar surfaces toward the ventral marginal groove of the inner demibranch (Figure 4a, arrows). Particles in the marginal groove are transported anteriorly along the ventral margin and then between the paired labial palps (ILP & OLP). Here they are carried, via the proximal oral groove (POG), to the mouth (M).

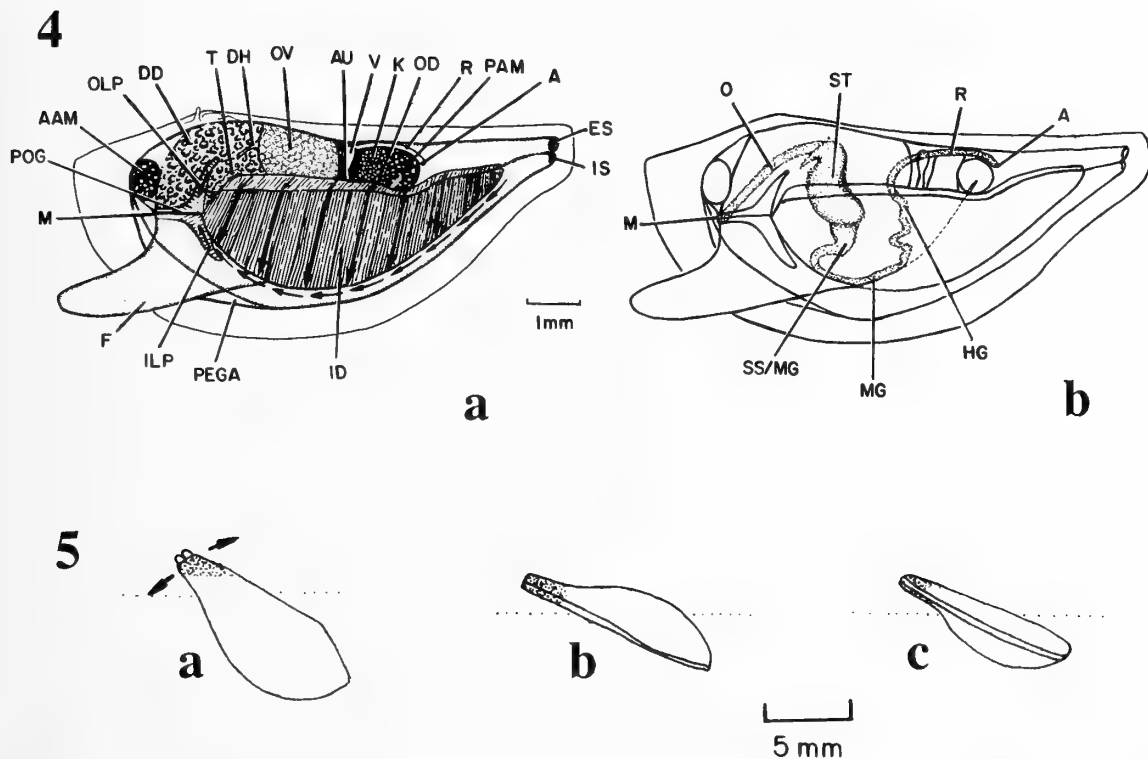
Organs of the Visceral Mass

Phoronis vesica is a simultaneous hermaphrodite. Paired ovaries (OV) are located dorsally, posterior to the digestive

diverticula (DD) and stomach (ST) (Figures 4a, b). Testes (T) exist on either side, beneath and slightly beyond the antero-dorsal region of the inner demibranch, over the digestive diverticula and ovary (Figure 4a). The esophagus (O) leads from the mouth to a stomach of type IV (Purchon, 1958, 1960) with a combined style sac and midgut (SS/MG) (Figure 4b). The dorsal hood (DH) is quite large and is visible on the left side beneath the mantle. The midgut (MG) quickly separates from the style sac and curves dorsally through the ovary. The rectum (R) is surrounded by a thin layer of connective tissue as it travels through the dorsal portion of the ventricle (V) of the heart. After passing between the dorsal lobes of the kidney (K), the rectum partially circles the posterior adductor muscle (PAM) and ends at the anus (A), which empties into the suprabranchial chamber near the exhalant siphon. The greenish-brown digestive diverticula (Figure 4a), located in the antero-dorsal region of the visceral mass, are connected to the stomach by ducts.

Burrowing

When living individuals were first placed upon the substratum, the foot was extended in a probing fashion. Sometimes, the foot was dug in and then used as a lever, allowing the animal to alter its position. More than half the animals



Explanation of Figures 4 and 5

Figure 4. a. The mantle cavity with ctenidial and palp currents as seen from the left side with mantle removed. b. Underlying organs of digestion in the mantle cavity as seen from the left side, shown with stippling. Solid lines indicate structures surrounding gut, visible beneath the mantle. Dashed line indicates outline of foot beneath the ctenidia. Key: A, anus; AAM, anterior adductor muscle; AU, auricle; DD, digestive diverticula; DH, dorsal hood; ES, exhalant siphon; F, foot; HG, hindgut; ID, inner demibranch; ILP, inner labial palp; IS, inhalant siphon; K, kidney; M, mouth; MG, midgut; O, esophagus; OD, outer demibranch; OLP, outer

labial palp; OV, ovary; PAM, posterior adductor muscle; PEGA, pedal gape; POG, proximal oral groove; R, rectum; SS/MG, conjoined style sac and midgut; ST, stomach; T, testes; V, ventricle.

Figure 5. a. Position of shell within substrate, dorsal side up. Arrows indicate rocking motion along the dorsal-ventral axis. b. Position of shell within substrate, left valve up. c. Position of shell within substrate, right valve up.

successfully buried themselves within 12 hours and achieved positions that deviated between 5° and 40° from the horizontal. The posterior end always protruded above the substratum. When burrowing was observed, the dorsal margin was oriented upwards in some cases (Figure 5a), the convex left valve uppermost in others (Figure 5b), and the flattened right valve uppermost in the remainder (Figure 5c). Individuals which buried themselves with the dorsal margin upwards were occasionally seen to rock slightly along the dorso-ventral axis (arrows, Figure 5a). Individuals buried with the right or left valve upwards tended to remain more exposed.

DISCUSSION

The shell structure of Atlantic species of *Pandora* has been described previously (Allen, 1954; Boss & Merrill, 1965). The inequivalve shell of *P. filosa* is similar to that of *P. inaequalis* and *P. pinna* (Allen, 1954). Dentition of the

valve hinge is much like that described by Allen (1954) for the eastern Atlantic species. The single tooth in the left valve (Figure 2) corresponds to the apomorphic character IX which Waller (1990) used to distinguish the Anomalodesmata. Boss & Merrill (1965) considered the dental patterns of *P. inaequalis* and *P. filosa* to be simple, as compared with western Atlantic species. The progressive change in length of the pallial muscle scars of *P. filosa* was not reported upon for *P. gouldiana* (Boss & Merrill, 1965).

The ligament of *Pandora filosa* has a lithodesma, which is absent in the two species of *Pandora* described by Allen (1954). The ligament is attached to the valves via resilifers as in the Lyonsiidae (Yonge, 1976). There is also a secondary ligament which consists of dorsally fused periostracum. Waller (1990) believed the anterior outer ligament of the anomalodesmatans (among others) to be not primary ligament, but rather material used to repair the separating umbones and splitting inner ligament. Yonge & Morton (1980) considered the common ligament type of the Lyon-

siidae, which is also seen in *P. filosa*, to be of early ancestry. They thought the dorsal-ventral rotation of the ligament of *P. grandis* to be a consequence of the lateral compression exhibited by various members of the family. *Pandora filosa* does not, however, display this rotated condition. An examination of *P. gouldiana* suggests that lateral compression, accompanied by rotation of the ligament, is markedly greater than that of *P. filosa*. Thus, the lesser degree of lateral compression displayed in *P. filosa* can be correlated with a lack of ligament rotation, as originally suggested by Yonge & Morton (1980).

The siphons of *P. filosa* resemble those of *P. gouldiana* (Boss & Merrill, 1965) and species of *Lyonsia* (Morse, 1919; Narchi, 1968). Tentacles surrounding the rim of the inhalant siphon are probably used to exclude large particles from the mantle cavity. The dark band surrounding the exhalant siphons of *Lyonsia californica* (Narchi, 1968) and *Lyonsia hyalina* (Prezant, 1977; personal observation) is absent in *Pandora*. Siphonal photosensitivity has been reported upon for representatives of at least one other family of the Pandoracea, i.e., the Lyonsiidae (Narchi, 1968). Withdrawal behavior, in response to a shadow, may be an anti-predation device. It is unlikely that this reflex is limited to only these two families of the Pandoracea since the posterior mantle margin assumed the former sensory function of the head in the Bivalvia (Allen, 1985).

Pandora filosa lacks a fourth pallial aperture as do other species within the Pandoridae (Allen, 1954; Boss & Merrill, 1965). Allen (personal communication) suspects that *Pandora* never possessed this structure. Three other families within the Pandoracea have members that possess a fourth pallial aperture: the Lyonsiidae (Yonge, 1952; Narchi, 1968), the Cleidothaeridae (Morton, 1974) and the Myochamidae (Morton, 1977). Boss (1978) reported that a loss of the fourth pallial aperture has occurred in members of various superfamilies within the Anomalodesmata. The function of the fourth pallial aperture is not understood. Yonge (1952) considered it to be a structural feature, dependent upon the way in which the mantle edges fuse during ontogeny. Allen (1985) thought it to be a pressure relief valve, a water jet for burrowing, or an opening for waste disposal. Morton (1985) suggested that the fourth pallial aperture acts as a relief valve in *Phalodomya* and concluded that its function is undetermined in other anomalodesmatans.

The mesial bulbus arteriosis of the ventricle reported upon by Boss & Merrill (1965) for *P. gouldiana* was not observed in *P. filosa*. The thin layer of ventricular tissue which surrounds the rectum in *P. filosa* does not constitute a bulb.

The triangular area observed near the byssal groove, which stains with methylene blue, is probably the non-functioning remnant of a byssal gland. The spat of *P. inaequalis* has a functioning byssal gland which later degenerates (Allen, 1961). Such may be the case with *P. filosa*, as it is likely to have a postmetamorphic juvenile

stage, when temporary attachment to the substratum may be necessary.

Pandora filosa is simultaneously hermaphroditic. This condition is believed to characterize the Anomalodesmata (Morton, 1981). Cross-fertilization is generally the rule in the Bivalvia (Mackie, 1984), though self-fertilization leading to normally developed eggs has been observed in the Lyonsiidae under laboratory conditions (Chanley & Castagna, 1966). Simultaneous hermaphroditism is the most common form of hermaphroditism in the Bivalvia. It is usually preceded by a period of protandry or in rare cases protogyny, which permits cross-fertilization at such a time (Mackie, 1984).

Allen & Allen (1955) concluded that *Pandora*, found in quiescent waters, most frequently is positioned in the substrate with the convex valve down and siphons exposed, as in Figure 5c. They suggested that slight scouring of these well-protected areas tends to uncover the valves and that increased wave activity during stormy periods tends to flip the shell over to a more stable position. The convex valve then becomes uppermost, a position thought to stimulate burrowing and subsequent reorientation (Allen & Allen, 1955). *Pandora filosa* is found in waters deeper than 18 m (Abbott, 1974) and, like *P. inaequalis*, inhabits low energy environments. Both species burrow and achieve similar orientations within the substrate. It is reasonable to predict that they will exhibit like behavior. *Pandora filosa* probably maintains itself in the favored near-horizontal position with the convex valve down and siphons slightly exposed.

ACKNOWLEDGMENTS

I gratefully acknowledge the following people and organizations for support in this endeavor: the California Malacozoological Society and the Western Society of Malacologists for sponsorship of the bivalve workshop where this work was performed; Paul H. Scott, Santa Barbara Museum of Natural History, California, for the invitation to participate in the workshop and his ongoing support; all of the participants of the WSM Bivalve Workshop for their encouragement, particularly Prof. Brian Morton, the University of Hong Kong, for his expert advice on functional morphology, biological drawing and general inspiration, and Dr. Eugene Coan, Santa Barbara Museum of Natural History, California, for access to his library; Dr. James Nybakken, Dr. Rikk Kvitek, and the staff of the Moss Landing Marine Laboratories, California, for the use of their facilities, equipment and samples; the Dr. Robert A. DeWolf Memorial Fund and the University of Rhode Island for financial support; Mr. Kenneth Davignon, University of Rhode Island, for pleasant answers to endless questions regarding technical illustration; Prof. John Allen, University Marine Station, Millport, Scotland, Dr. Robert B. Hill, University of Rhode Island and two anonymous reviewers for their criticism of the first

draft of this manuscript; Dr. Robert C. Bullock, University of Rhode Island, for his ongoing encouragement, provision of samples, and review of the manuscript. A very special thanks is extended to the Teraji family of Castroville, California, for their wonderful hospitality and great cheer. For Christine, Jonathon, Mary and Sharon.

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International Workshop on the Marine Bivalvia of California

Axinopsida serricata (Carpenter, 1864),
Its Burrowing Behavior and the Functional Anatomy
of Its Pallial Organs (Mollusca: Thyasiridae)

by

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Abstract. Small, probably juvenile specimens of the northeastern Pacific thyasirid *Axinopsida serricata* (Carpenter, 1864) were dredged off Moss Landing, California. The activity of the foot, pallial folds and apertures, the ciliary currents of the inhalant pallial chamber, and the burrowing behavior of live animals <3 mm in shell length were observed. These characters, together with those related to the gross morphology of the pallial organs and viscera, were compared with those recorded for other thyasirid species.

INTRODUCTION

The small thyasirid *Axinopsida serricata* (Carpenter, 1864), originally placed in the genus *Cryptodon*, inhabits the coastal waters of northwest America, having been recorded from Alaska (Bernard, 1983) to California, USA and Baja California, Mexico (Palmer, 1958; Bernard, 1983), with its type locality designated as Puget Sound, Washington by Palmer (1958). Populations of this variable species have been distinguished by differences in the ranges of their height/length ratios and of their size, reaching a larger size (with a thicker periostracum) in colder waters where they occupy a greater depth range. To some of these populations the names *Cryptodon* (*Clausina*) *suborbicularis* A. Adams, 1862, *Cryptodon* (*Clausina*) *subquadratus* A. Adams, 1862, and *Axinopsida viridis* Dall, 1901, have been applied.

MATERIAL EXAMINED

With the assistance of the director and staff of the Moss Landing Research Laboratories and using that laboratory's research vessel R/V *Ricketts*, twenty-two specimens of *Axinopsida serricata* were taken using a Smith MacIntyre grab and an epibenthic sled on 6 and 11 July 1991 off Moss Landing, California, at about 36°49'N, 121°50'W in depths of 30 and 60 m (WAM 220.93 to 223.93). These specimens ranged in size from 1.47 to 2.8 mm in shell

length and were maintained in aquaria. The four largest specimens, of shell length greater than 2.6 mm, were used for anatomical study, and the behavior of these and the smaller specimens was observed over several days.

Specimens of this species in the collections of the California Academy of Sciences, San Francisco (CAS 542515, 41603, 379/1, 374/2), collected from off the coasts of southern and central California, showed a greater size range, with some specimens reaching 4.8 mm in shell length. Specimens from the southern coasts of Alaska in the collections of the Museum of the University of Alaska (1987-1, 1985-8, 77-78) are larger still, with shell lengths up to 8 mm.

Morphology (Figures 1, 2, & 3)

Shell: The shell outline is variable. It tends to be almost circular with the shell length almost equal to its height, although some specimens are slightly more elongate. The umbo is small, pointed and prosogyrate, and the antero-dorsal (lunular) and postero-dorsal edges of the right valve overlap those of the left. The valves lack any suggestion of a radial sulcus, and their degree of convexity increases with size.

The shell is smooth exteriorly, marked with few growth lines. The valves of smaller living specimens are transparent. Those of larger specimens are more opaque, par-

ticularly along the area of the pallial line, and contain white chalky patches. These patches are generally located in more dorsal areas, and are irregular in position, size, and number. The distal areas of most larger dead specimens are evenly opaque. The free edges of the valves of the live specimens examined are uncalcified, consisting of a relatively wide band of the colorless, transparent, and shining periostracum. The periostracum is thicker and of a yellowish color in most larger specimens previously collected in Alaskan waters. In the antero-dorsal area of the external surface of each valve, there is usually a patch of a yellow-brown accretion. This is more often present in larger specimens which may also have a similar postero-dorsal patch.

The hinge lacks true cardinal teeth, but has a pseudo-cardinal tubercle below the right umbo, and a more anterior pseudocardinal ventral to the somewhat sunken lunule on the left valve (Figure 1). The ligament is sunken below the postero-dorsal margin.

Pallium: The inner and middle pallial folds are simple and lack sensory and guard tentacles. The dorsal pallial isthmus terminates anteriorly at a level approximately opposite the dorsal end of the anterior adductor muscle to form the antero-dorsal edge of the pedal aperture (Figure 3a). The most anterior and posterior sections of the pedal aperture are defined as inhalant apertures by adhesion of the inner pallial folds (Figures 2, 3a, b). Fusion of the inner pallial folds forms a connective bridge at the level of the posterior ends of the ctenidial axes and divides the posterior inhalant aperture from the more dorsal exhalant aperture (Figures 2, 3b). A fusion of the inner pallial lobes forms the dorsal rim of the exhalant aperture opposite the posterior adductor muscle, and the middle pallial folds unite just dorsal to this point to form the posterior end of the pallial isthmus.

A pair of small muscular lappets projects from the middle pallial folds midway along the connective bridge ventral to the exhalant aperture.

Foot: (Figures 2, 3a, c): The elongate base of the muscular foot extends ventrally from the visceral mass and is laterally compressed. It narrows abruptly to form a long, narrow cylinder, the vermiform foot, which tapers only just proximally to its tip. Both portions of the foot are transversely wrinkled when contracted.

Ctenidia (Figure 2): The fragile, transparent ctenidia extend antero-dorsally to postero-ventrally. The anterior ends of the ctenidial axes are located in the dorso-lateral extensions of the pallial cavity inside the beaks of the valves, just postero-lateral to the umbones. The posterior ends of the gills are located anterior to the connective bridge which divides the inhalant from the exhalant aperture. There are approximately 34 filaments in both the wider inner and the narrower outer demibranchs in a specimen of shell length 2.4 mm, and about 50 in one 4.1 mm long. The

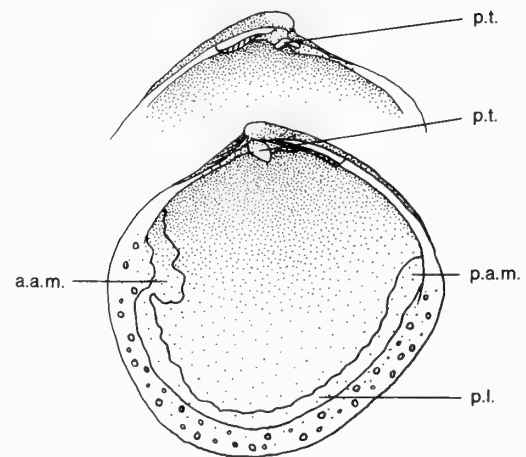


Figure 1

A. serricata: Interior of left (above) and right (below) shell valves, to show: scar of anterior adductor muscle (a.a.m.), scar of posterior adductor muscle (p.a.m.), pallial line (p.l.), pseudocardinal tubercles (p.t.).

filaments are firmly united by tissue junctions, although the inter-lamellar connections are few.

The anterior gill filaments are fused to the distal oral groove. Food grooves run along the ctenidial axes and the ventral edges of the inner demibranchs. Anterior to the bases of the posterior pedal retractor muscles, the gill axes and the tips of the ascending lamellae of both pairs of demibranchs are fused to the visceral mass. Posterior to these muscles, the ascending limbs of the inner demibranchs adhere to one another mid-ventrally, and the tips of the ascending limbs of the outer demibranchs, the most posterior gill filaments, and the gill axes adhere to the membranous walls of the exhalant chamber. This chamber extends posteriorly beneath the posterior adductor muscle, to which it is attached dorsally. Distally the walls of the chamber are continuous with the rim of the exhalant aperture.

Labia: The mouth is posterior to the dorsal section of the anterior adductor muscle and located between the basal sections of the anterior pedal retractor muscles. The horizontal upper oral lip is suspended from tissue bands which attach it to the posterior surface of the anterior adductor. It is wider than the lower lip which is attached directly to the anterior pedal retractors. Dorso-laterally to the mouth, the lips are narrow, expanding only slightly to form short, narrow labial palps at about the level of the free edges of the inner demibranchs. The palps of the lower lip are slightly wider and extend a little more ventrally than do those of the upper lip. In the specimens examined, the palps have about three indistinct low folds on their inner surfaces.

Visceral Pouches: Diverticula of the digestive gland are located in large, lobular lateral pouches which project into the inhalant pallial chamber (Figure 2). These visceral

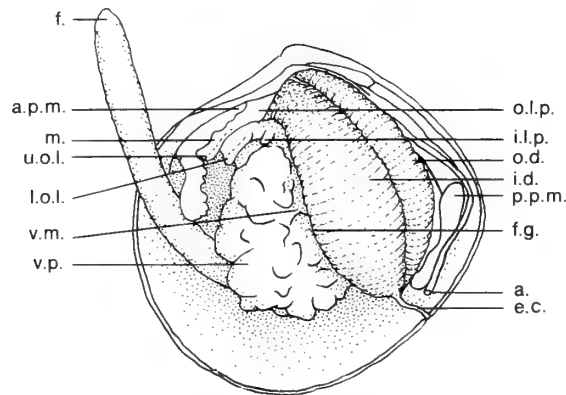


Figure 2. *A. serricata*: Left side with left shell valve and pallial lobe removed to show: anus (a.), anterior pedal retractor muscle (a.p.m.), membranous floor of exhalant chamber (e.c.), foot (f.), marginal food groove on inner demibranch (f.g.), inner demibranch (i.d.), inner labial palp (i.l.p.), lower oral lip (l.o.l.), position of mouth (m.), outer demibranch (o.d.), outer labial palp (o.l.p.), posterior pedal retractor muscle (p.p.m.), upper oral lip (u.o.l.), visceral mass (v.m.), visceral pouch (v.p.). Other labels as in Figure 1.

pouches are connected on each side with the visceral mass, and internally with the stomach, by narrow stalks. In the live specimens examined, the pouches were brown until placed in formalin, after which they soon lost their color. The size of these pouches is relatively greater, and the development of their lobes is more marked in larger, broader specimens. This might be related, at least in part, to the growth of the gonadal tissue covering the digestive tubules within.

Alimentary Canal: The gut is simple. Close to its origin at the posterior of the large stomach, the short intestine bends sharply to run antero-dorsally to a point just under the umbones. Here it again bends sharply to run posteriorly through the ventricle and dorsal to the large auricles and the kidneys. The rectum is attached to the distal surface of the posterior adductor muscle and projects just beyond

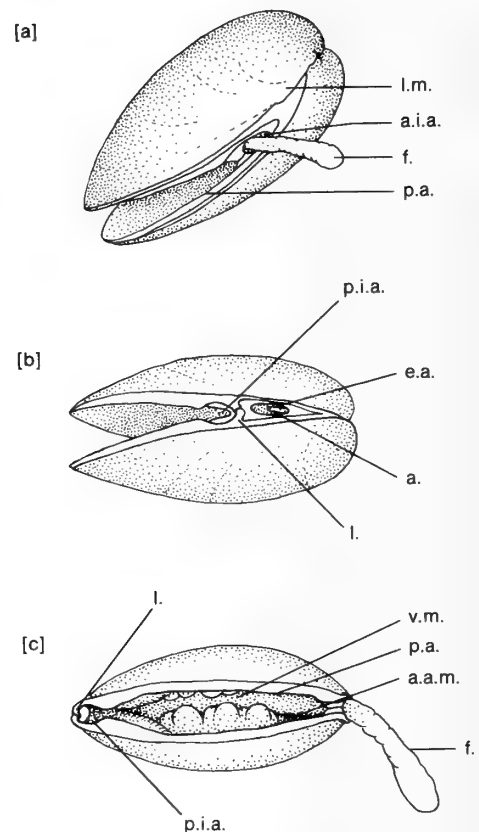


Figure 3. *A. serricata*: Antero-dorsal (a), posterior (b) and ventral (c) views to show: anterior inhalant aperture (a.i.a.), right lappet (l.), expanded right lunular shell margin (l.m.), pedal aperture (p.a.), foot (f.), posterior inhalant aperture (p.i.a.). Other labels as in Figure 2.

its ventral end so that the anus is washed by the exhalant current (Figure 2).

Observations of Live Specimens

Pallial Cavity: In unburied specimens, the outer and middle pallial folds bordering the anterior inhalant section of the pedal aperture were observed to be held almost permanently agape. Infrequently, the inner folds in this area separated symmetrically, or sometimes slightly asymmetrically, to temporarily open the aperture.

Slightly dorsal of the ventral end of the anterior adductor muscle, there is a narrow zone where temporary adhesion occurred between the inner pallial folds. This zone of adhesion separates the anterior inhalant section from the remainder of the pedal aperture.

The length and shape of the pedal aperture changed

continually. The pallial folds and attached periostracum, held at right angles to the calcified portions of the shell valves and acting as a curtain, moved together as the radial muscles of the right and left pallial lobes contracted and expanded. The pedal aperture opened as a result of the contraction of one or both pallial folds.

The ventral limit of the posterior inhalant aperture is formed by the temporary juxtaposition of the pallial folds over a variable distance. This aperture was observed to open only during the burying cycle. It then opened briefly on one side, before closing suddenly as a sudden contraction of the pedal and presumably, of the adductor muscles occurred. In unburied specimens, it is improbable that an inhalant current could pass regularly through this rarely opened aperture, although a swift intake of water could occur during the burying cycle. No protrusion of any of the apertural lips was observed.

Strong ciliary action, directed toward the postero-ventral area of the inhalant chamber, was observed on the mantle epithelium. The ciliary action was particularly strong below and above the anterior adductor muscle and on the epithelium of its exposed surfaces. Even more active were the cilia on the epithelium of the visceral pouches, particularly on their more medial surfaces. In specimens from which one shell valve and adjacent pallial lobe had been removed, mucus-bound particulate matter tended to accumulate just dorsal to the free end of the anterior adductor muscle and ventral to the posterior tips of the gills. It is presumed that in normally active, intact specimens this material would have been moved postero-ventrally. Although the expulsion of pseudofeces was not observed, it seems likely to occur through the posterior inhalant aperture which is adjacent to the site of pseudofecal accumulation within the inhalant pallial chamber.

Foot: In small animals with transparent shells, the foot can be seen moving within the inhalant pallial chamber. Lateral movement of the distal end of the foot was commonly observed near the anterior inhalant aperture, ventral and anterior to the anterior adductor muscle.

The vermiform section of the foot of live, unburied specimens was observed to extend to no more than four times the diameter of the shell. The slightly tapered tip was faintly transversely wrinkled, and occasionally and for short periods the section just proximal to the tip was observed to thicken very slightly. However, in specimens which had been narcotized for about 15 hours in seawater mixed with an isotonic solution of sodium chloride, the foot developed a variably shaped expansion at its tip. In such specimens, the foot was normally extended but, apart from the tip, was more slender than was usual.

Burrowing Behavior (Figure 4): When placed flat on a sand surface, specimens of *A. serricata* extended the foot through the pedal aperture, which temporarily opened to a length slightly greater than the diameter of the foot. The foot could be extended through the pedal gape at any

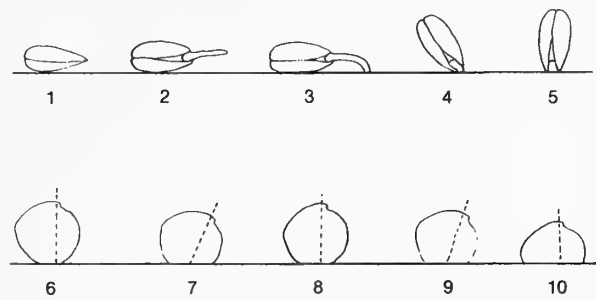


Figure 4

A. serricata: Diagram of sequence of movements involved in burrowing, viewed initially from the front (1-5) and then from the right side (6-10), with 5 and 6 being synchronous.

position to and including the anterior inhalant aperture, but it was never observed to intrude into the area of the posterior inhalant aperture.

The tip of the extended foot touched the sediment surface at a few points and then began to probe into the sediment adjacent to the ventral shell lip. An extremely fine sheet of mucus secreted by and encircling the tip of the foot was seen to move proximally, presumably propelled by ciliary and/or muscular action. Some smaller sand particles were carried with it.

The foot probed more deeply, and the bivalve was abruptly lifted to the vertical position, to "sit" with its longitudinal hinge axis approximately parallel to the sediment surface. The shell was then repeatedly rocked anteriorwards to about 30° from the vertical and then back to the resting position, never to a position posterior to this. At this moment, the posterior inhalant aperture was seen to open and close. Each sequence resulted in a descent further into the substrate. When not obstructed, five or six cycles resulted in the complete burial of the shell/body of an animal of about 2.5 mm shell length.

Despite repeated attempts, the burrowing actions in the vertical plane within the sediment could not be observed. When confined to thin layers of sediment between vertical glass walls so that they could be viewed from the side, the tiny animal remained motionless. It is possible that the rapidly increasing temperature of the water and substrate adjacent to the animal inhibited this activity. When the apparatus was placed in the cold water aquarium tank, burying was accomplished and proceeded to a depth of about four to six times the depth of the shells over about eight hours. After four days, a mucus tube had formed, similar to those formed by lucinid species observed by Allen (1953). It projected from the shell margin in the region of the yellow accretion and the anterior inhalant aperture. However, in these specimens of *A. serricata*, the very fragile, transparent tube was not visible *in situ* and could be seen only when an animal could be disinterred without dislodging the tube. It is possible that the mucus tubes and their attachment to the bivalves become more robust with

time, as they are reinforced with extra layers of mucus. No sand grains were found attached to these mucus tubes.

When the animals were placed on sediment in petri dishes within cold water baths, they remained active. Their burrowing behavior could then be observed, though only from above. If the sediment layer was too shallow to allow complete burial, the animals burrowed horizontally, even when the shell was completely or partially exposed above the sediment surface. During this horizontal burrowing, the shell was usually held "upright" i.e., dorsal side uppermost, although such burrowing was occasionally accomplished with the anterior or the posterior side uppermost. Even in these positions, the same sequence of burying movements was used, with the shell/body being rotated to the anterior and then to the resting position relative to the extended foot.

DISCUSSION

Recent studies of thyasirids (Nakazima, 1958; Soot-Ryen, 1966; Bernard, 1972, 1982) emphasized the importance of research on this and other lucinacean families by Allen (1958). Payne & Allen (1991), with their work on 25 species and three subspecies of thyasirids from the deep Atlantic, have more precisely defined the family and a number of its subfamilial taxa. They demonstrated the importance of anatomical characters, such as the form and presumably, the functioning of the ctenidia, the form of the vermiform section of the foot, and the shape of the lobes of the lateral body pouches in clarifying taxonomic divisions previously based on shell characters alone.

The ctenidia of *A. serricata*, comprising two sets of demibranchs, more closely resemble those of the genus *Axinus* and the subgenus *T. (Parathyasira)* than of other forms in which the outer demibranch is reduced or lost (Payne & Allen, 1991). Differing noticeably from the thick brown ctenidia of *Thyasira flexuosa* (Montagu, 1803) (Allen, 1958) with their large vacuolated cells which contain bacteria (Reid & Brand, 1986), and those of *Axinus grandis* Verrill and Bush, 1898, and *T. (T.) excavata* Dall, 1901, with their strong abfrontal extensions of the ctenidial filaments (Payne & Allen, 1991), the fragile colorless ctenidia of the specimens of *A. serricata* from off Moss Landing give no indication that sulfide-oxidizing symbiotic bacteria might be contained within them. This is consistent with the observation by Reid & Brand (1986) that the large vacuolated cells in the ctenidia of specimens of this species from off Vancouver Island, Canada did not contain bacteria. In *T. flexuosa*, by contrast, these authors found abundant bacteria in the vacuoles of similar cells in the ctenidia as well as the enzymes characteristic of sulfide-oxidizing symbiosis.

The degree of fusion of the tips of the anterior ascending limbs of the inner demibranchs to the visceral mass appears to vary among thyasirid species. In *A. serricata* there is tissue fusion, as Bernard (1972) indicates for *T. disjuncta*

(Gabb, 1866) and as is observed for *A. serricata*. Weaker ciliary adhesion in *T. flexuosa* is described by Allen (1958).

The relative size of the labial palps of *A. serricata* appears to be even smaller than those of most *Thyasira* species examined by Allen (1958) and Bernard (1972, 1982) except perhaps those of *T. orecta*, a new species described by Bernard in 1982 from deep water off the coast of Washington, USA. Reduction in size and complexity of the labial palps of lucinaceans has been associated by Allen (1958) with the increased efficiency of the particle-sorting mechanism in the anterior inhalant pallial chamber, related to the presence of the anterior inhalant current (Payne & Allen, 1991).

The fused pallial folds above and below the exhalant aperture do not bear paired papillae like those in *Thyasira flexuosa*, which Allen (1958) presumed to have a sensory function, and those examined by Bernard (1972) in *T. cygnus* Dall, 1917. Instead, the connecting bridge forming the ventral margin of the exhalant aperture of *A. serricata* bears a pair of thin lappets which can extend distally or can contract to fold and overlap medially (Figure 3b, c). The function of these lappets is unknown.

The degree of definition of a posterior inhalant aperture in *A. serricata* is apparently similar to that observed by Payne & Allen (1991) in a number of thyasirid species. It is not known whether this aperture is formed in *A. serricata* by mantle adhesion as they described in *Axinus grandis*, or by interlocking ciliary pads on the middle fold as in various species of *Thyasira (Parathyasira)* described by those authors.

There was no suggestion in live specimens of *A. serricata* of any demarcation of the terminal part of the foot as described for *Thyasira* s.s. by Allen (1953, 1958), Bernard (1972, 1982) and Payne & Allen (1991) or the presence or formation, under normal circumstances, of a terminal expansion or bulb as described for species of the *Thyasira* subgenera *Parathyasira*, *Axinulus*, *Leptaxinus*, and *Mendicula* by Payne & Allen (1991). The terminal expansion formed by specimens of *A. serricata* being narcotized does not seem to resemble that recorded for any other thyasirid species.

The extended foot of the California specimens examined was observed to be shorter than that of *T. flexuosa* as described by Allen (1953, 1958) and of *T. bisecta* (Conrad, 1849) described by Bernard (1972). In the larger preserved specimens from Alaska, the foot appeared to be relatively shorter. Payne & Allen (1991) indicate that the foot of species of *Thyasira*, other than those species of relatively large size placed in the nominate subgenus, seems to be shorter. Foot length is apparently related to the depth to which the animal can bury itself. As in other species of *Thyasira*, the vermiform foot *A. serricata* can be accommodated in the inhalant pallial cavity only in a bent position.

It is possible that the foot and a number of other organs of this and other thyasirid species exhibit allometric growth

and that the possibly immature specimens of *A. serricata* examined here cannot be validly compared with presumably mature species of other species. Comparative developmental and ecological studies are needed for this and other thyasirid species.

ACKNOWLEDGMENTS

I wish to thank Mr. P. Scott, Professor B. Morton and Dr. E. Coan for organizing and running the bivalve workshop so efficiently and enthusiastically. The cheerful assistance of Dr. J. Nybakken and his staff was much appreciated. The interest and cooperation of other workshop participants was contagious, including that of Ms. N. Foster of the University of Alaska who, with the staff of the California Academy of Sciences, kindly made specimens available to me on loan. In addition, I have greatly appreciated the constructive criticism of the anonymous reviewers of this manuscript.

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International Workshop on the Marine Bivalvia of California

On the Anatomy of the Alimentary Tracts of the
Bivalves *Nemocardium* (*Keenaea*) *centifilosum*
(Carpenter, 1864) and *Clinocardium nuttallii*
(Conrad, 1837) (Cardiidae)

by

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Abstract. The labial palps, ctenidia, stomach interior, intestine, tentacles, and siphons of the proto-cardiine *Nemocardium* (*Keenaea*) *centifilosum* (Carpenter, 1864) and the clinocardiine *Clinocardium nuttallii* (Conrad, 1837) were examined to determine their morphology. Although they are broadly similar anatomically, the digestive system of *C. nuttallii* is more complex than that of *N. centrifilosum*. The inner demibranch of *N. centrifilosum* inserts into the oral groove between the labial palps, whereas in *C. nuttallii* the inner demibranch attaches to the dorsal extension of the inner palp. The supra-axial extension of the outer demibranch is more strongly developed in *C. nuttallii*. The stomach of *N. centrifilosum* lacks a dorsal hood sorting area. The intestine of *C. nuttallii* is longer and more complex.

INTRODUCTION

Although the family Cardiidae has been the subject of considerable taxonomic study, nearly all work on cardiid morphology has considered only the shell. Besides the numerous studies of the edible cockle *Cerastoderma edule* (Linné, 1758) and the light receptors of cardiids, only Pelseneer's (1911) monograph stands out as a source of information on the anatomy of the Cardiidae. (For references on cardiid taxonomy, anatomy of *C. edule*, and cardiid light receptors, see Schneider [1992]). As part of a detailed phylogenetic study of the Cardiidae (Schneider, 1993), the gross anatomy of the cardiids *Nemocardium* (*Keenaea*) *centifilosum* (Carpenter, 1864) and *Clinocardium nuttallii* (Conrad, 1837) was examined. Special attention was paid to the labial palps, ctenidia, stomach interior, gut, tentacles, and siphons, as these structures have been shown to be the most phylogenetically informative (Schneider, 1992, 1993).

MATERIALS AND METHODS

Specimens of *Nemocardium* (*Keenaea*) *centifilosum* were collected at a depth of 55 meters with a Smith-McIntyre grab (11 specimens), and at a depth of 80 meters with an otter trawl (111 specimens), on 6 July 1991, off the coast of Moss Landing from sandy, organic-rich muds in Monterey Bay, California. Specimens were brought back to the Moss Landing Marine Laboratories, relaxed with magnesium chloride, and studied both alive and after fixation in 5% formalin in seawater. Collected specimens of *N. centrifilosum* ranged from 1.3 to 8.0 mm shell length. Twelve specimens were dissected. Voucher specimens of *N. centrifilosum* were deposited in the Santa Barbara Museum of Natural History, SBMNH 35526. Four specimens of the clinocardiine *Clinocardium nuttallii*, ranging from 38.8 mm to 49.1 mm in shell length, were collected by hand on 13 July 1991, at low tide from muddy silts on an exposed tidal flat of Elkhorn Slough, Moss Landing, California. One specimen was relaxed with magnesium chloride and studied alive. One specimen was studied after being relaxed and then fixed in 5% formalin in seawater. Two additional specimens (Field Museum of Natural History [FMNH])

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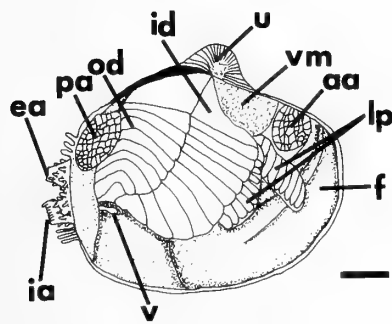


Figure 1

Nemocardium centifilum, external anatomy, as shown from the right side with right valve and right mantle removed. Key: aa, anterior adductor; ea, excurrent aperture; f, foot; ia, incurrent aperture; id, inner demibranch; lp, labial palps; od, outer demibranch; pa, posterior adductor; u, umbo; v, valvule; vm, visceral mass. Scale bar equals 1 mm.

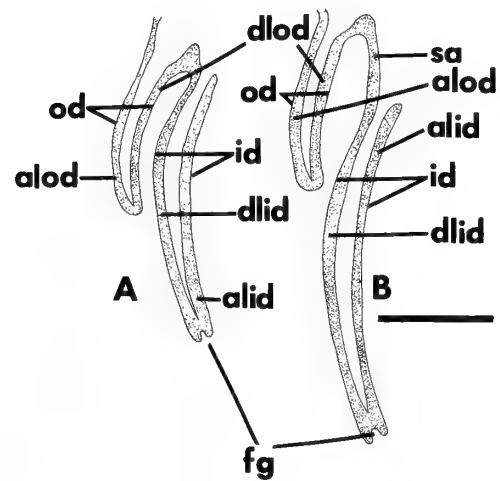


Figure 3

Diagrammatic vertical section of ctenidia of two different individuals of *Nemocardium centifilum* to show location of food grooves (fg) and variation in supra-axial extension (sa) from essentially no supra-axial extension (A) to a considerable supra-axial extension (B). Key: alid, ascending lamella of inner demibranch; alod, ascending lamella of outer demibranch; dlid, descending lamella of inner demibranch; dlod, descending lamella of outer demibranch; fg, food groove; id, inner demibranch; od, outer demibranch; sa, supra-axial extension. Scale bar equals 1 mm.

RESULTS

Nemocardium (Keenaea) centifilum (Carpenter, 1864)

(Figures 1–6)

The labial palps (Figure 2) are roughly triangular in shape, with opposing sets of ridges on the outer surface of the inner palp and inner surface of the outer palp. The palp-ctenidia connection is of Stasek's (1963) type II, in which the ventral tips of the anteriormost filaments of the inner demibranch are inserted and fused to a distal oral groove. The anterior end of the inner demibranch inserts

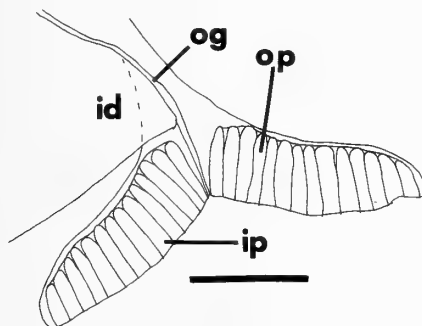


Figure 2

Labial palps (right side) of *Nemocardium centifilum* and their connection with ctenidia. Palps folded back so that ridge-bearing inner surfaces face reader. Anterodorsal portion of inner demibranch attaches behind inner demibranch (id) and is represented by dashed line. Key: id, inner demibranch; ip, inner labial palp; og, oral groove; op, outer labial palp. Scale bar equals 1 mm.

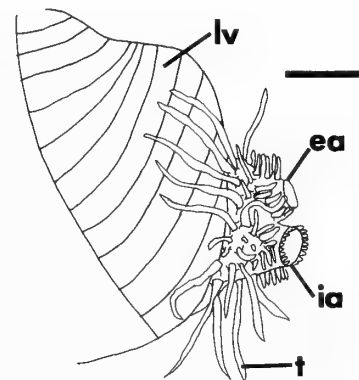


Figure 4

Siphons and tentacles of *Nemocardium centifilum*, as seen from left side. Key: ea, excurrent aperture; ia, incurrent aperture; lv, left valve; t, tentacle. Scale bar equals 1 mm.

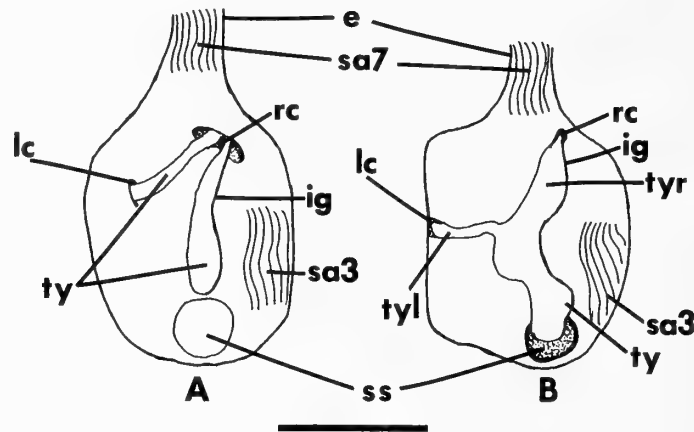


Figure 5

Stomach floor of protocardines. Figure 5A. Stomach floor of *Nemocardium bechei*, redrawn from Nakazima (1964). Figure 5B. Stomach floor of *Nemocardium centifilosum*. Key: e, esophagus; ig, intestinal groove; lc, left caecum; rc, right caecum; sa3, posterior sorting area; sa7, esophageal sorting area; ss, style sac; ty, major typhlosole; tyl, left branch of major typhlosole; tyr, right branch of major typhlosole. Scale bar equals 1 mm, no scale was included by Nakazima (1964).

(1937) gill type C1, ranged from essentially non-existent (Figure 3A) to pronounced (Figure 3B). There was no correlation between size of the animal and extent of the supra-axial extension.

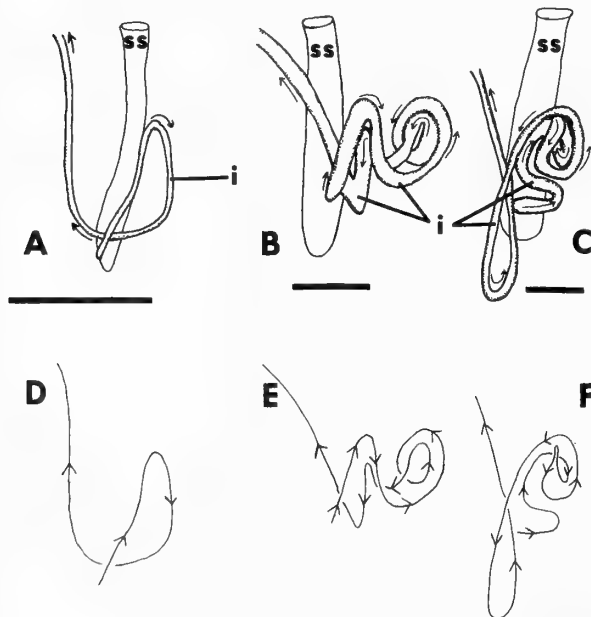


Figure 6

Three representative intestines of *Nemocardium centifilosum*, as seen from right side. Arrows indicate path of intestine, from base of style sac to exit of intestine from visceral mass. A, B, and C are drawings of intestine and style sac; D, E, and F are schematic depictions of intestinal paths of A, B, and C, respectively. Key: i, intestine; ss, style sac. Scale bars all equal 1 mm.

The ctenidia are weakly plicated. The inner demibranch bears between seven and 15 plicae, and the outer demibranch between six and 11 plicae. The posterior and anterior ends of the outer demibranch are not plicated, the most distal plicae being composed of considerably more filaments (20 to 40) than the intermediate plicae (10 to 12). In the case of the inner demibranch, the wide anteriormost plica is composed of 10 to 15 filaments. The other plicae of the inner demibranch, although narrower, are composed of a similar number of filaments (10 to 16). Attempts to remove one valve and keep the animal alive to analyze ciliary currents and labial palp activity were unsuccessful.

The stomach of *Nemocardium centifilosum* is of Purchon's (1960) type V, in which the major typhlosole and intestinal groove penetrate both the left and right caeca. The stomach is very shallow, taking up only the very top of the visceral mass. The digestive diverticula lie directly beneath the stomach. In *Nemocardium bechei* (Reeve, 1847) (Figure 5A; see Nakazima, 1964), the major typhlosole emerges from the style sac and traverses the center of the stomach floor, penetrates the right caecum, re-emerges from the right caecum, and then traverses posteriorly across the left side of the stomach floor and enters the left caecum. *N. centifilosum* (Figure 5B) is similar to *N. bechei* in the relative positions of the caeca, but the path of the major typhlosole differs. In *N. centifilosum*, instead of a single wide loop, the major typhlosole splits into two branches midway across the stomach floor, with one branch (tyr) continuing across the middle of the stomach and entering the right caecum. The other branch (tyl) traverses the left side of the stomach and enters the left caecum. As in *N. bechei* (see Nakazima, 1964, and Kafanov & Popov, 1977), there is a posterior sorting area (SA3; see Purchon [1960]

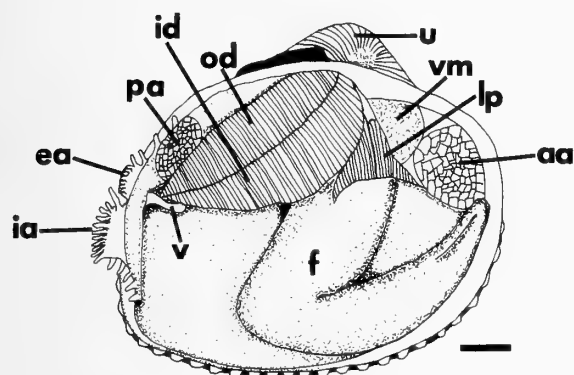


Figure 7

Clinocardium nuttallii, external anatomy, viewed from the right side with right valve and right mantle removed. Key: aa, anterior adductor; ea, excurrent aperture; f, foot; ia, incurrent aperture; id, inner demibranch; lp, labial palps; od, outer demibranch; pa, posterior adductor; u, umbo; v, valvule; vm, visceral mass. Scale bar equals 5 mm.

for terminology of the sorting areas in bivalve stomachs), an esophageal sorting area (SA7), but no dorsal hood sorting area (SA8).

In the smallest specimens, the intestine consists of a single loop (Figure 6A, D). During ontogeny, the intestine loops two or three times, although the path of the gut is variable (Figure 6A–F). The intestine was unraveled in one specimen (Figure 6C, F; shell length 5.35 mm) to determine its length. From the base of the style sac to the exit from the visceral mass, the intestine was 5.05 mm in length. The intestine is enveloped by gonadal tissue. After exiting the visceral mass, the intestine enters the pericardium and passes through the middle of the ventricle of the heart, continues along the dorsal body wall above the posterior adductors, and terminates in the anus.

The pericardium, heart, and kidneys are similar to those described by Johnstone (1899) for *Cerastoderma edule* and by White (1942) for *Maoricardium setosum* (Redfield, 1846). The pericardium occupies the dorsal portion of the body between the posterior of the visceral mass and the posterior adductors. The heart consists of a single median ventricle and two auricles. Ménégau (1890) and Pelseneer (1911) have noted the near uniformity of the structure of the heart within the Cardiidae.

The siphons (Figure 4) are of Yonge's (1982) type A+. Yonge (1982) introduced this siphonal type to describe the unique form of mantle fusion in the Cardioidea. The middle fold of the mantle margin is greatly reduced, and the sensory tentacles and light receptor organs are carried on the inner folds, which alone constitute the siphons. In other bivalves with tentacles and sensory organs, these structures are formed of the middle mantle fold. A semicircular flap of tissue, called alternatively the languette or curtain valve by Dall (1889), and the valvule by Pelseneer (1911) and Schneider (1992, 1993), is present on the interior of the

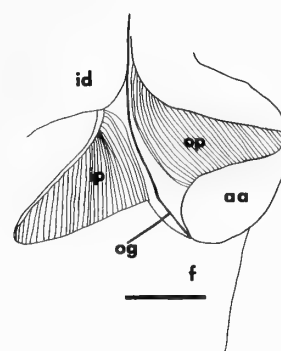


Figure 8

Labial palps (right side) of *Clinocardium nuttallii* and their connection with the ctenidia. Key: aa, anterior adductor; f, foot; id, inner demibranch; ip, inner palp; og, oral groove; op, outer palp. Scale bar equals 5 mm.

siphonal apparatus, just dorsal to the incurrent aperture (Figure 1, v). The rim of the incurrent aperture is ringed by approximately 30 small tentacles, whereas the rim of the excurrent aperture bears no tentacles. The tentacles are simple, and present from the pedal gape dorsally to just beyond the bottom of the posterior adductors. Contrary to the situation found in the cardiid *Fulvia hungerfordi* (G.B. de Sowerby III, 1901) by Reid & Shin (1985), there is neither differentiation amongst the tentacles of the rim of the incurrent aperture into larger and smaller palps, nor is there differentiation amongst the posterior mantle tentacles in discrete sets of dorsal, ventral, and small and large lateral tentacles. The total number of posterior mantle tentacles is approximately 120.

Clinocardium nuttallii (Conrad, 1837)

(Figures 7–12)

As in *Nemocardium centifilum*, the labial palps (Figure 8) are triangular in shape, but are not as long relative to their height (morphological features were found to be consistent among the live-collected specimens and the FMNH specimens). The palps carry approximately 30 ridges. *Clinocardium nuttallii* was Stasek's (1963) example of a type II palp connection. Unlike *N. centifilum*, the anterior portion of the inner demibranch does not attach between the labial palps, but to the dorsal extension of the inner palp. The palps are relatively larger than in *N. centifilum*, being approximately one-third the length of the inner demibranch.

As in other cardiids, the ctenidia (Figure 9) are Atkins' (1937) type C1. Only the inner demibranch bears a food groove. The supra-axial extension of the outer demibranch is more pronounced than in *Nemocardium centifilum*. The outer demibranch is approximately two-thirds as high as the inner demibranch, and approximately nine-tenths as long. The ctenidia of *Clinocardium nuttallii* are much more

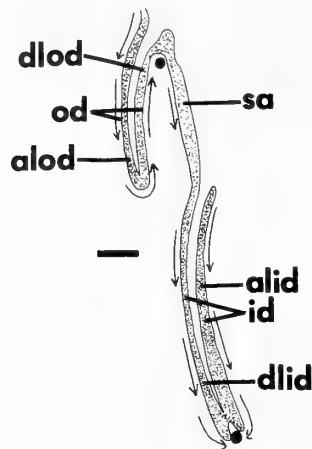


Figure 9

Diagrammatic vertical section through ctenidium of *Clinocardium nuttallii* to show direction of beat of cilia, see Kellogg (1915) and Atkins (1937). Key as in Figure 3. Scale bar equals 5 mm.

strongly plicated than those of *N. centifilosum*. The outer demibranch bears from 53 to 120 plicae, and the inner demibranch bears from 75 to 110 plicae. Each plica bears approximately 40 filaments. The ciliary currents of *C. nuttallii* were analyzed; results were identical to those described by Kellogg (1915).

The stomach (Figure 10) is of Purchon's (1960) type V. Unlike *Nemocardium centifilosum*, the digestive diverticula envelop the stomach, rather than simply being located beneath the stomach. The middle of the stomach floor, between the style sac and the esophagus, is raised relative to the rest of the stomach floor (rb, raised bar). The major typhlosole (ty) emerges from the style sac and traverses anteriorly across the raised bar. Anterior of the raised bar, the major typhlosole bifurcates. The narrower branch of the major typhlosole enters the centrally located right caecum. The wider branch enters the more anteriorly and laterally located left caecum. There is a posterior sorting area (SA3) and an esophageal sorting area (SA7).

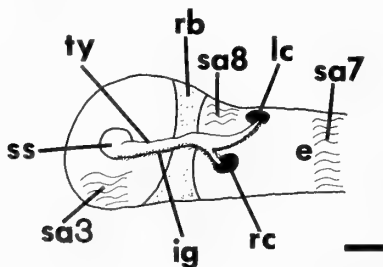


Figure 10

Stomach floor of *Clinocardium nuttallii*. Key: e, esophagus; ig, intestinal groove; lc, left caecum; rb, raised bar; rc, right caecum; sa3, posterior sorting area; sa7, esophageal sorting area; sa8, dorsal hood sorting area; ty, major typhlosole.

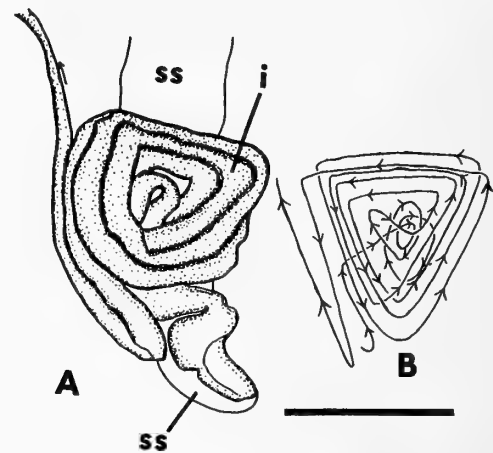


Figure 11

Intestine of *Clinocardium nuttallii*. A. Appearance of intestine (i) when viewed from right side. B. Schematic diagram of intestinal pathway, indicated by arrows. Key: i, intestine; ss, style sac. Scale bar equals 5 mm.

Unlike *Nemocardium bechei* and *N. centifilosum*, the dorsal hood sorting area (SA8) is present, as Kafanov & Popov (1977) reported.

The intestine (Figure 11) of *Clinocardium nuttallii* is more complex than in *Nemocardium centifilosum*. As seen from the right side, the intestinal path was virtually identical in all specimens examined. This is contrary to *N. centifilosum*, in which the intestinal path is variable, even in specimens of similar size (as stated previously, no juvenile specimens of *Clinocardium nuttallii* were available for examination). The exact path of the intestine was determined in the specimen (shell length 38.8 mm) that was

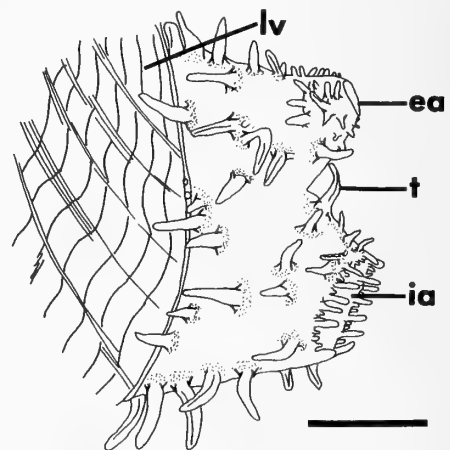


Figure 12

Siphons and tentacles of *Clinocardium nuttallii* as seen from left side. Key: ea, excurrent aperture; ia, incurrent aperture; lv, left valve; t, tentacle. Scale bar equals 5 mm.

examined alive. The intestine consists of 11 loops. The length of the intestine, from the base of the style sac to the exit of the intestine from the visceral mass, is 300 mm. The intestine was enveloped by gonadal tissue. Gallucci & Gallucci (1982) found that *C. nuttallii* is dioecious. The pericardium and heart are similar to *N. centifilum*.

DISCUSSION

I know of only two other accounts of the anatomy of species of *Nemocardium*: the description of the stomach of *N. bechei* by Nakazima (1964) and Dall's (1889) description of the siphonal apparatus of *N. (Lophocardium) annettae* Dall, 1889. In contrast, *Clinocardium nuttallii* is one of the few commonly studied cardiids (Kellogg, 1915; Stasek, 1963; Silvey, 1968; Gallucci & Gallucci, 1982). Although neither *N. centifilum* nor *C. nuttallii* is highly derived anatomically (Schneider, 1993), there are phylogenetically important differences that can be noted between them.

The digestive system of *Clinocardium nuttallii* is more complex than that of *Nemocardium centifilum*. The labial palps of *C. nuttallii* are larger relative to the ctenidia, and the ctenidia are more plicate and are composed of more filaments. The labial palp-inner demibranch relationship in *N. centifilum* is the primitive condition in cardiids (Schneider, 1993), in which the anterior of the inner demibranch attaches between the inner and outer labial palps. This condition is illustrated by *Cerastoderma edule*, *Acanthocardia (Rudicardia) tuberculata* (Linné, 1758), and *Cardium indicum* (Lamarck, 1819) (see Foster-Smith, 1975; Thiele, 1886; Deshayes, 1848). The condition in *C. nuttallii*, in which the inner labial palps attach to the ventral edge of the inner demibranch, is derived. This latter inner demibranch-labial palp relationship is clearly illustrated by Kellogg (1915).

According to Purchon (1960), the most important aspect of the bivalve stomach from a phylogenetic point of view is the path of the major typhlosole. In both *Clinocardium nuttallii* and *Nemocardium centifilum*, the major typhlosole bifurcates, with one branch entering the left caecum and the other branch entering the right caecum. This condition is unlike that of other illustrated cardiid stomachs, namely *N. bechei* (see Nakazima, 1964) and *Cerastoderma edule* (see Graham, 1949). In the latter two species, the major typhlosole does not bifurcate, but first enters the right caecum, re-emerges onto the stomach floor, then enters the left caecum. Likewise, in the Cardiidae, often considered the sister taxon to the Cardiidae (Keen, 1969, 1980; Schneider, 1992), the major typhlosole does not bifurcate, but forms a spiral fold in the middle of the stomach floor (Pelseneer, 1911; Purchon 1958; personal observation). Non-bifurcation of the major typhlosole is the primitive condition, whereas bifurcation is derived. The dorsal hood sorting area is present in cardiids (Purchon, 1958) and all cardiids (Graham, 1949; Purchon 1960; Kafanov & Popov, 1977), except for the protocardiines *N. bechei*

and *N. centifilum*. Absence of this sorting area is a derived condition of protocardiines.

Quite striking is the difference in the intestine between the two species, with the intestine of *Clinocardium nuttallii* containing 11 loops as opposed to one to three for *Nemocardium centifilum*, and the intestine in *C. nuttallii* being more than eight times longer in length relative to the animal. The difference between the two species in complexity of the intestine should not be attributed to their size difference, for (1) many species comparable in size to, or even much smaller than, *N. centifilum* have the same form of intestine as *C. nuttallii*, and (2) other, larger species of *Nemocardium* have the same intestine as *N. centifilum* (Schneider, 1993). The intestinal path of *N. centifilum* is comparable to that found in cardiids (Heaslip, 1968; Yonge, 1969) and represents the primitive condition in the Cardiidae (Schneider, 1992, 1993). Variability in the intestinal path of bivalves is not unusual, as Jones (1979) found noticeable intraspecific variability in the intestinal path of several venerids.

The siphonal apparatus of *Clinocardium nuttallii* (Figure 12) is the characteristic A+ type of cardioids (Yonge, 1982). As in *Nemocardium centifilum*, a valvule (Figure 7, v) is present. There are considerably fewer posterior mantle tentacles (60 versus 120) on *C. nuttallii* than on *N. centifilum*, especially dorsal to the excurrent aperture. Dorsally, the tentacles on *C. nuttallii* are present to the top of the posterior adductors. In contrast to *N. centifilum*, there is some differentiation in *C. nuttallii* amongst both the tentacles of the incurrent aperture and those of the posterior mantle. Along the rim of the incurrent aperture, there is a larger tentacle followed by between one to three smaller tentacles. The posterior mantle tentacles on the base of the excurrent aperture are smaller than the other posterior mantle tentacles. Although *N. centifilum* has approximately twice as many tentacles as *C. nuttallii*, the dorsalmost location of the tentacles is more dorsal on *C. nuttallii* (to the top of the posterior adductors) than on *N. centifilum* (just beyond the bottom of the posterior adductors). There is no correlation between density of tentacles and how far dorsally they extend.

ACKNOWLEDGMENTS

This project was undertaken during the marine bivalve workshop hosted by the Moss Landing Marine Laboratories from July 5–19, 1991. I would like to thank P. Scott of the Santa Barbara Museum of Natural History for organizing the workshop and J. Nybakken of the Moss Landing Marine Laboratories for allowing use of the laboratory's facilities. Specimens of *N. centifilum* were collected while on board the R/V *Ricketts*. The manuscript was improved by comments by D. W. Phillips, R. Bieler, and three anonymous reviewers. During part of my graduate study I was supported by NSF grant EAR-90-05744 to D. Jablonski.

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International Workshop on the Marine Bivalvia of California

The Genus *Parvilucina* in the Eastern Pacific:
Making Evolutionary Sense of a Chemosymbiotic
Species Complex

by

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Abstract. Understanding the evolutionary history of lucinoidean bivalve chemosymbiosis requires robust hypotheses of phylogeny that map features onto clearly defined taxa. Studies of lucinoidean chemosymbiosis to date have not had adequate taxonomic grounding. The genus *Parvilucina* in the eastern Pacific illustrates the need to bring new anatomical, ecological, biochemical, and geochemical data into a systematic framework. New observations of live specimens of the type species (*P. tenuisculpta*) from disaerobic sediments in the Monterey Canyon and reevaluation of collections of minute lucinids from the eastern Pacific suggest that the type species is actually part of a species complex, with at least three morphologically distinct members. Scanning electron micrographs illustrate the features of the hingeline and shell ornamentation that distinguish *P. mazatlanica* and *P. approximata* from the type species. Differences in shell morphology and locality data underlie a prediction that these two species do not live directly in reduced sediments and are distinctive in their ecology and physiology.

Sedimentary, geochemical, and biogeochemical settings of the California Borderlands provide a model system in which to characterize the complexity of lucinoidean chemosymbioses. The generalization that lucinoidean symbioses are thiotrophic, based on reduced sulfur, embraces a broad spectrum of potential morphologic and biochemical adaptations. Potential adaptations follow from the range and placement of usable reduced sulfur compounds in the environment and include: (1) the range of metabolic pathways in the bacterial symbionts using these compounds; (2) the range of requirements placed upon the sulfur metabolism of the host bivalve in the uptake, transport, and housing of compounds of varying toxicity; (3) methods of housing the symbionts; and (4) the bioenergetics of translocation of fixed carbon products from symbiont to host.

INTRODUCTION

Lucinoidean bivalve species form dense populations in a variety of marine habitats and may dominate marine invertebrate communities in numbers of individuals and biomass. Interest in the basic biology of living lucinoideans has been stimulated considerably by the discovery of several structurally and physiologically distinctive relationships between endosymbiotic autotrophic sulfur-oxidizing prokaryotes and the gills of many species in the families Thyasiridae (Southward, 1986; Dando & Southward, 1986; Reid & Brand, 1986; LePennec et al., 1988; Wood &

Kelly, 1989) and Lucinidae (Felbeck et al., 1981; Cavanaugh, 1983; Berg & Alatolo, 1984; Fisher & Hand, 1984; Dando et al., 1985, 1986; Giere, 1985; Schweimanns & Felbeck, 1985; Reid & Brand, 1986; Vetter, 1985; Southward, 1986; Spiro et al., 1986; Distel & Felbeck, 1987; LePennec et al., 1988; Cary et al., 1989b). The possibility that lucinoideans have other types of symbionts, such as methylotrophic prokaryotes (Wood & Kelly, 1989) bears further investigation.

Inference of chemosymbiosis in lucinids follows from many different lines of evidence: (1) assay of gill extracts identifying enzymes concerned with the fixation of carbon

dioxide (e.g., ribulosebiphosphate carboxylase and phosphoribulokinase); (2) assay of gill extracts identifying enzymes involved in the oxidation of sulfur (e.g., adenylylsulphate reductase and adenylyltransferrase); (3) transmission electron microscopic illustration of prokaryotic inclusions in the vacuoles of eukaryotic "bacteriocytes"; (4) energy dispersive x-ray analysis of air-dried, freeze-fractured gills and energy dispersive spectrophotometry showing sulfur as the dominant inorganic element in gill tissue; (5) experiments with incubated gill tissue measuring rates of metabolism of labeled sulfide; (6) experiments with incubated gill tissue measuring fixation rates of ^{14}C carbon dioxide with and without sulfide; (7) determination of a chemosymbiotic signal in the ratios of stable carbon isotopes ($^{13}\text{C}/^{12}\text{C}$) in bivalve tissue; and (8) actual isolation of symbionts from gill tissue and characterization of them as distinctive and taxon-specific in terms of their 16S rRNA gene sequences (Distel et al., 1988; Eisen et al., 1992).

Distel & Felbeck (1987) have shown that the lucinid gill is organized into three structurally and functionally distinct zones, with normal ctenidial function of blood ventilation and particle filtration confined to the outer ctenidial filament zone and chemosymbiosis confined to the innermost bacteriocyte zone. Distel & Felbeck (1987) suggest that this organization and mode of nutrition are pervasive throughout Lucinidae, raising an interesting question of the evolutionary history of chemosymbiosis in a family whose evolutionary origins allegedly date from the Silurian Period (Chavan, 1969). See Appendix A for a guide to terms used in discussing molluscan chemosymbioses.

The most recent focus of interest in lucinid chemosymbiosis is on its biogeochemical detection in the fossil record, providing the first direct evidence bearing on the evolutionary history of chemosymbiosis in lucinid lineages and the history of communities dominated by this trophic strategy. Hickman (1984) designated an Eocene–Holocene *Thyasira*–*Lucinoma*–*Solemya* Community from numerous recurring active margin bathyal fossil assemblages dominated by different species of these three bivalve genera and suggested the presence of parallel communities in the Cretaceous. Campbell (1989, 1992) and Campbell & Bottjer (1990 and in press) subsequently recognized this as a suspect chemosymbiotic bivalve community and have developed elegant field and laboratory protocols for identifying, characterizing, and classifying ancient chemosymbiotic habitats. Campbell has demonstrated that many suspect chemosymbiotic assemblages (including fossil mytilid and vesicomyid bivalves) are associated with masses of microbial carbonates that represent ancient cold seeps. Her field studies have further identified structural evidence of potential conduits for fluid flow, and her laboratory analyses of the carbonates show the appropriate carbon isotopic signatures for cold seeps.

Focusing on the lucinid bivalve component of chemosymbiotic communities, CoBabe (1991, 1992, and unpublished) has demonstrated that the organic matrix of the

shell is a good isotopic proxy for the living tissue and that the shells of living and fossil lucinids yield isotopic signatures ($\delta^{13}\text{C}$) of chemosynthesis. This is a potentially powerful direct approach to questions of the evolution of lucinoidean chemosymbiosis. It decouples the study of history from assumptions of taxonomic uniformitarianism and opens up questions of multiple derivations and losses of chemosymbiotic relationships to direct testing. It is dependent upon well-preserved shell material and will not discriminate chemosymbiosis from ingestion of chemosynthetic organic compounds from the environment. It does, however, represent a first step in detection of metabolic pathways in the bivalve as well as in the surrounding environment.

Burgeoning interest in the evolutionary history of lucinid chemosymbiosis unfortunately has not been accompanied by reevaluation of lucinid systematics. Although species names are applied to all of the taxa that have been investigated in studies of chemosymbiosis, none of the authors cited above has figured shells, designated hypotypes, or mentioned repositories for voucher specimens. It is noteworthy that the family Lucinidae (*sensu lato*), with the most derived ctenidial structure (a well-developed bacteriocyte zone, intracellular housing of symbionts, and inferred loss of one of the two pairs of demibranchs), has a considerably earlier putative origin (Silurian) than the less derived Thyasiridae (Middle Triassic), while the Ungulinidae (Diplodontidae *auctt.*), retaining the primitive ctenidial condition and lacking chemosymbionts, is geologically youngest (Upper Cretaceous). Interpretation of the fossil record of these families must be reevaluated.

Conflicting interpretations help focus the need for careful phylogenetic analysis of well-delineated monophyletic taxa. Evolutionary understanding of lucinid chemosymbiosis will not be resolved by spinning adaptive scenarios. Scenarios must be tested against rigorous hypotheses of lucinid relationships: maps of evolutionary novelties on taxa. It is especially important that studies of ultrastructure, physiology, and functional anatomy be firmly grounded taxonomically if novel features are to be associated correctly with taxa.

The importance of delineating monophyletic lineages and taxa is illustrated by the genus *Parvilucina* in the eastern Pacific. There are three available names that have been applied to forms of *Parvilucina* from the northeastern Pacific. However, many authors follow Bretsky (1976) in recognizing a single, highly variable species, most commonly identified as *Parvilucina tenuisculpta* (Carpenter, 1864). The latitudinal range of *P. tenuisculpta* is reported as Alaska (60°N) to Baja California (32°N) (Keen, 1937). How many species of *Parvilucina* are there in the eastern Pacific?

Chemosymbiosis is reported from specimens identified as *P. tenuisculpta* from British Columbia (Reid & Brand, 1986) to southern California (Felbeck et al., 1981) and from environments ranging from offshore silts rich sulfides (Reid & Brand, 1986) to nearshore sewage outfalls (Fel-

beck et al., 1981). Museum specimens (Hickman, personal observation) identified as *P. tenuisculpta* also are reported from diverse settings in the California Borderlands that include the mainland shelf, the dysaerobic margins of anoxic basins, and insular shelves and sediment-starved ridges of the California Channel Islands. Many of the reported localities do not suggest distinctive "sulfide biotopes." Although most museum lots are from less than 100 meters, live-collected animals come from stations as deep as 450 meters. Jones & Thompson (1984) identified specimens from 226 stations in the southern California Borderlands as *P. tenuisculpta*, but did not designate voucher specimens for these localities. With increasing evidence of multiple trophic resources, alternative metabolic pathways, and different kinds of bacteria involved in bivalve chemosymbioses (e.g., Fisher et al., 1987; Cary et al., 1989a; Fisher, 1990), it is clear that we cannot begin to make evolutionary sense of the minute lucinids in the eastern Pacific until we can associate metabolic pathways and microhabitats with correctly identified taxa.

The same caveat applies to understanding the genus *Parvilucina* worldwide. Endosymbiotic bacteria are reported from the gills of minute-shelled (3 mm) specimens identified by Giere (1985) as *Parvilucina multilineata* Toumey and Holmes, 1857, in a detailed study of the structure and position of bacteriocytes within the gill epithelia. Again, no voucher specimens were designated, and the detailed data presented by Giere cannot be mapped with assurance onto taxa.

The purpose of this paper is (1) to focus issues of lucinoidean systematics and evolutionary history that have been ignored during a period of rapid advance in knowledge of lucinoidean functional anatomy and metabolic physiology; (2) to report some observations of live-collected, typical *Parvilucina tenuisculpta* from 60 meters in the Monterey Canyon; (3) to provide scanning electron micrographic illustration of what I interpret as three distinct species of *Parvilucina* from the eastern Pacific; (4) to provide morphological criteria for distinguishing *Parvilucina* species; and (5) to discuss the morphological disparity of these species in relationship to lucinoidean chemosymbiosis and the variety of settings on the active margin of the North American continent that provide the critical access to both reduced chemical compounds and molecular oxygen.

BIOLOGY AND SYSTEMATICS OF LUCINIDAE

Lucinid Biology: The Historical Perspective

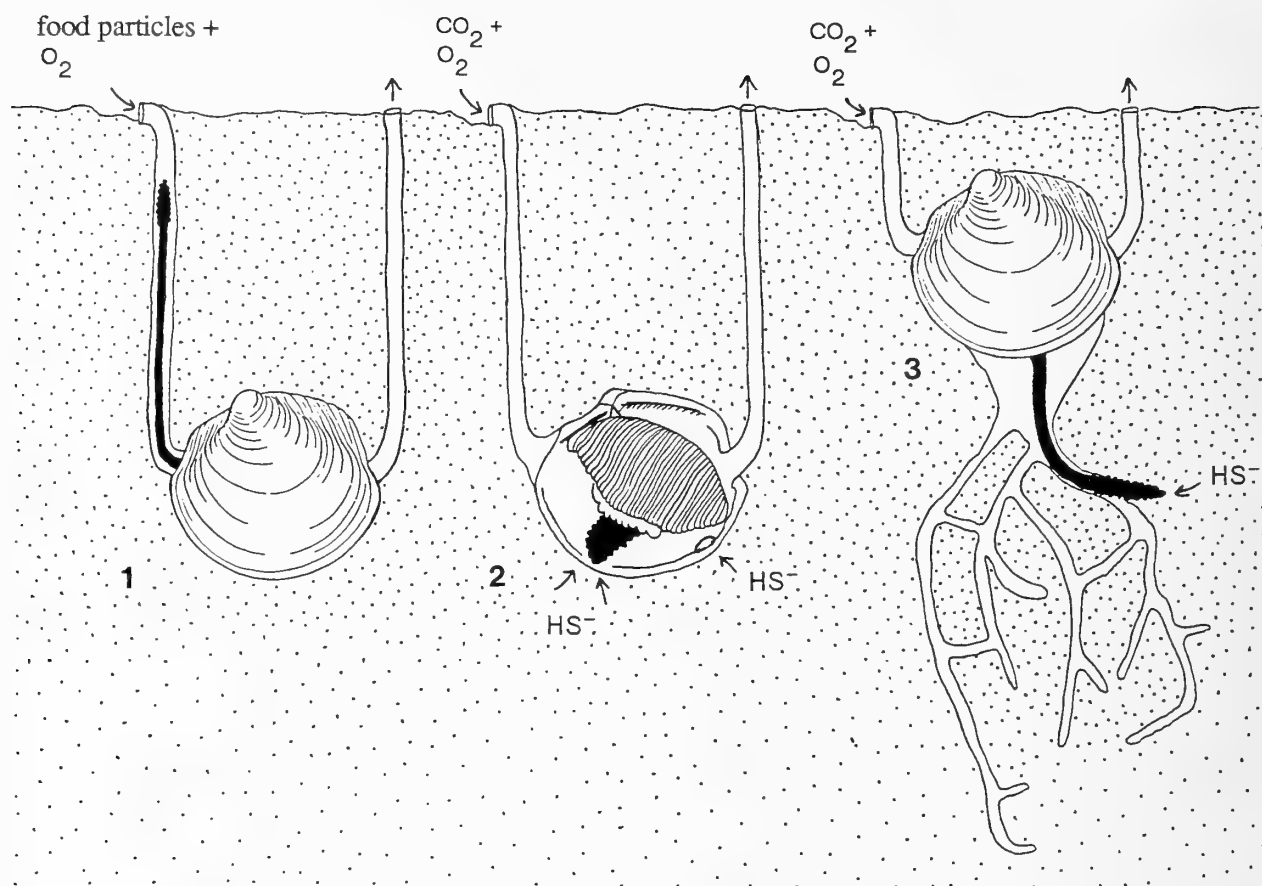
The discovery of chemosymbioses in lucinid and thyasirid bivalves has affected interpretations of the basic biology and evolutionary history of the entire superfamily. Understanding of the functional anatomy and ecology of lucinid bivalves is based primarily upon the work of Allen (1958, 1960), who emphasized the enlargement and thick-

ening of the gills, reduction of the labial palps coupled with loss of particle sorting capabilities, and reduction of gut length and simplification of the stomach. Allen's study is a classic in functional anatomy. It also includes functional accounts of burrowing, use of the foot in construction of the anterior inhalant tube, and details of ciliary currents on the body.

Allen's (1958) conclusion that lucinids inhabited marginal habitats and had adopted an unselective macrophagous habit, underlies the conventional interpretation of the group as competitively inferior (see Bretsky, 1976, p. 123, and references therein). Prior to the recognition of lucinid chemosymbiosis, this was a logical ecological interpretation. However, it was difficult to reconcile competitive inferiority paleontologically with post-Paleozoic trends in the superfamily. Primitive lucinoideans not only survived the post-Paleozoic radiation of the presumably superior siphonate eulamellibranchs (Stanley, 1968), they paralleled it with a dramatic Mesozoic and Cenozoic radiation of their own.

The pre-chemosymbiosis view of lucinid ecology is summarized in Figure 1, where the vermiform portion of the foot is viewed primarily as a structure for constructing and maintaining the inhalant mucus tube. Two alternative interpretations of the evolutionary relationship of lucinids to other lucinoideans are depicted in Figures 4, 5. Allen (1958) viewed the three major lucinoidean families as stages in progressive simplification and loss of structure, and developed an evolutionary scenario in which unguinids are the closest to the primitive eulamellibranch and lucinids are the most derived (Figure 4). This trend is the reverse of the order of first appearance of lucinoidean families in the fossil record as recorded in the Treatise on Invertebrate Paleontology (Chavan, 1969). Boss (1969) recognized the problem with the fossil record and reversed the scenario. He further recognized the similarity of fimbriids and lucinids and suggested that the two were primitive sister taxa. Under this interpretation, the geologically younger thyasirids and unguinids are represented as secondarily developing an outer demibranch and moving the superfamily independently back in the direction of typical eulamellibranch specializations (Figure 5). It is easier to map chemosymbiosis onto Allen's scenario as a synapomorphy of Thyasiridae + Lucinidae: it is derived once and is secondarily lost in some thyasirids. However, as we shall see below, the evolution of chemosymbiosis may have involved multiple innovations and losses, and all scenarios merit closer scrutiny and rigorous testing.

Chemosymbiosis provides a partial explanation of the evolutionary success of the family and alters the earlier view of competitive inferiority. It also may alter McAlester's (1966) view of the group as an evolutionary dead end. Reid & Brand (1986) introduce the bold and intriguing suggestion that chemosynthetic function of the bivalve gill might have been an essential precursor to the evolutionary shift from labial palp deposit feeding to suspension feeding. They argue that the primitive bivalve gill enlarged



Explanation of Figures 1 to 3

Three alternative views of lucinid orientation and life habit. Figure 1. A prechemosymbiosis view in which the function of the foot (solid black) is depicted as forming and maintaining the anterior inhalant mucus tube as a conduit for oxygen and large food particles (based on Allen, 1958; Hickman, 1984). Figure 2. A post-chemosymbiosis view in which the anterior tube is depicted as a conduit for oxygen for the lucinid and carbon dioxide for the symbionts, and the pedal gape and posterior inhalant opening are depicted as potential points of entry of reduced sulfur for photosymbionts (based on Reid & Brand, 1986). Figure 3. A post-symbiosis view in which the anterior tube also is depicted as a conduit for oxygen and carbon dioxide, but the shell is situated in oxygenated sediment and the foot is probing to locate pockets of biogenic sulfide or probing reduced sediments to facilitate diffusion of sulfide into the burrow system (based on Dando & Southward, 1986).

to accommodate endosymbionts and that its enlargement was the necessary precursor of its co-option for other roles.

Two post-chemosymbiosis views of lucinid ecology are summarized in Figures 2 and 3, and a new interpretation of evolutionary relationships is depicted in Figure 6. All of the ecological cartoons contain accurate information, but in my estimation none of them speaks for the entire superfamily. The evolutionary scenarios all contain some elements of strong support, but the real test is yet to come, in the form of a character analysis using all available data and many more taxa.

Figure 6 depicts the possibility that chemosymbiosis, in some crude form, is plesiomorphic to bivalves, where it might have begun through bacterial colonization of the exterior surface of the gills. In this interpretation, the

Paleozoic lucinoideans that have been identified in the past as lucinids are actually a primitive stem group in which taxa might have experimented with endocytosis of bacteria off the surface of the gill. This relationship was subsequently lost in Ungulinidae and further elaborated in the other two families. Internalization of the bacteria might be viewed as the next step in elaboration and regarded as a synapomorphy of Thyasiridae + Lucinidae. One form of extracellular bacteriocyte is an autapomorphy of Thyasiridae, and another form of intracellular bacteriocyte is an autapomorphy of Lucinidae s.s.

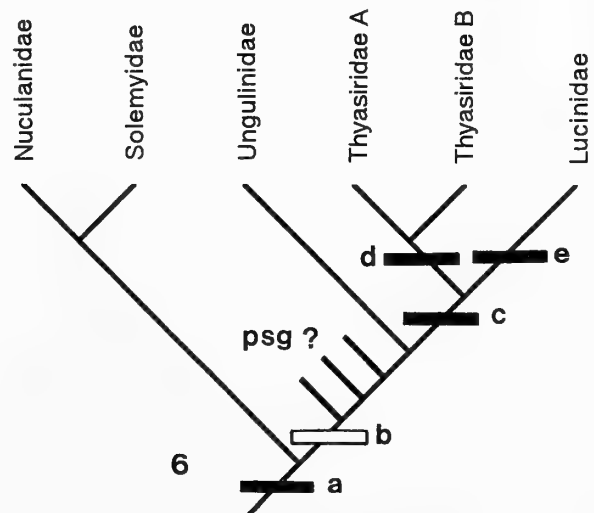
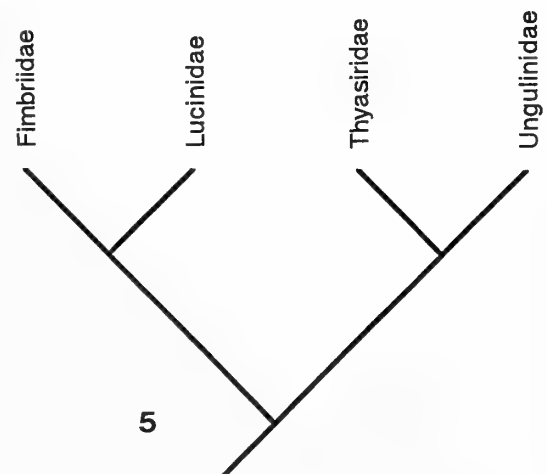
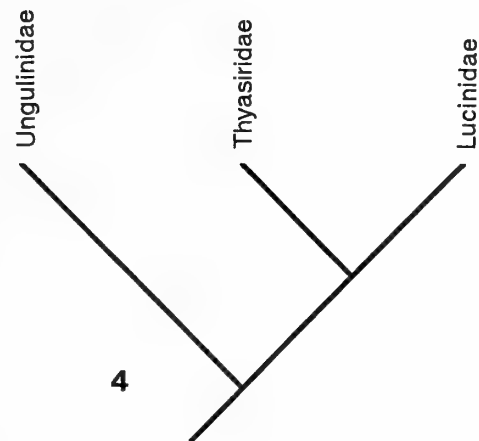
However, specialized chemosymbiosis as a universal lucinid feature does not provide a full explanation of either the diversity of shell form or the diversity of habitats occupied by lucinids, although there is tendency to generalize

this nutritional mode to a lifestyle to the entire superfamily (e.g., Seilacher, 1990). Allen's (1958) characterization of lucinids as the end member in a progression toward specialized ingestion of large particles in food-poor environments was based on the study of nine species in six genera. It has been generalized to all lucinids. The replacement view of all lucinids as chemosymbiotic bivalves is based on documentation of chemosymbiosis in approximately 14 species in eight genera. It is time to take a closer look at other genera. For example, Morton (1979) has shown that *Fimbria fimbriata* (Linnaeus, 1758), a common inhabitant of tropical clean coral sands, lives at the sediment-water interface, does not build an anterior inhalant mucus tube, and engages in pedal feeding (see Reid et al., 1992, for a recent review of pedal feeding in bivalves).

Lucinid Biology: Chemosymbiosis as a Potential Character Set

What bearing does chemosymbiosis have on lucinoidean systematics? It is generally treated as a single feature that is either present or absent (gained or lost). The language of chemosymbiosis does not translate readily into characters and character states, but the wealth of data in the literature suggests that this is an evolving relationship that shows considerable variation in its evolutionary expression. The purpose of this section is to suggest, in systematic terms, how some of this variation could be expressed in character analysis.

A first step in making evolutionary sense of the data from studies of chemoautotrophic symbioses is to tackle problems of homology. For example, use of the term "bacteriocyte" to describe how bacteria are housed within a bivalve host masks a fundamental difference between the intracellular, membrane-bounded bacteriocytes of lucinids and the extracellular but sub-cuticular bacteriocytes of thyasirids. Appendix 2 summarizes some of the features



Explanation of Figures 4 to 6

Three alternative hypotheses of lucinoidean relationships. Figure 4. The traditional interpretation of Allen (1958) in which lucinids are viewed as the most derived and ungulinids, the least derived. Figure 5. The interpretation of Boss (1969), recognizing fimbrids and lucinids as a less derived sister group of thyasirids and ungulinids. Figure 6. A post-chemosymbiosis interpretation based in part upon the suggestion by Reid & Brand (1986) that symbiotic relationships arose initially in more primitive bivalves. This view involves multiple losses of chemosymbiosis (in most nuculoideans, ungulinids, and some thyasirids), and permits chemosymbiosis to be established as a complex adaptation through a series of discrete innovations. a. represents establishment an external relationship between symbiont and gills; b. represents hypothetical specialization of the relationship in a lucinoidean Paleozoic stem group (psg). c. represents internalization of bacteria in the gill as a synapomorphy of Thyasiridae + Lucinidae. d, e. represent the organization of two different kinds of bacteriocytes as autapomorphies.

that are known to vary in thyasirid and lucinid chemosymbioses and suggests how they might be expressed as characters and character states. In determining their potential as characters, it will be important to eliminate any that are environmentally determined rather than phylogenetically based. The features are discussed briefly below.

Descriptions and illustrations in the literature documenting the location and housing of bacterial symbionts suggest at least seven potential characters. The first distinction is between extracellular and intracellular housing of the bacterial symbionts. In thyasirids, masses of bacteria are extracellular, occurring beneath the cuticular surface of the gill and above an underlying cell (Southward, 1986). The bacteriocyte, as illustrated by Southward, consists of the mass of bacteria, the overlying cuticle, and the underlying cup-shaped cell. In lucinids, the bacteriocyte is a specialized type of gill cell in which the symbionts occur within the membrane-bounded vesicles (Distel & Felbeck, 1987). Arrangement of the bacteriocyte cells in the species of *Lucinoma* and *Lucina* examined by Distel and Felbeck involves stacking of cells into cylinders with central hollow channels lined with intercallary cells with dense microvillae. As summarized by Fisher (1990), there are differences of opinion as to whether bacteriocytes in some lucinid species are exposed directly to seawater (i.e., with no covering of intercallary cells), as well as differences of opinion as to whether the bacteriocytes themselves have microvillae on their surfaces or are smooth. It is unclear whether the differences arise from the preparation and interpretation or whether they represent different structural states. If complicated three-dimensional structure of the bacteriocyte zone has evolved through accumulation of evolutionary novelties, we might expect to see different structural configurations in living lucinids. Other features in which variation is reported include the size of bacteriocyte cells, the shapes of bacteriocyte cells, and the numbers of bacteria per membrane-bounded vesicle within bacteriocyte cells (Fisher, 1990 and references therein).

In addition to the nature of the housing of symbionts, there are aspects of host regulation of the relationship that are potentially useful as systematic characters. There appears to be some variation in the size of the populations of live bacteria maintained by the bivalve host (large or small) and variation in the number of endosymbiont types present. Most of the variation seems to be in thyasirids, where it is not simply a matter of the presence or absence of symbionts, but a more complex situation in which some species maintain large populations and others maintain small populations (Southward, 1986). There is also variation in the number of symbiont types present within a host species. The most commonly reported state is one symbiont type per host, but Southward (1986) reports two symbiont morphologies in a pair of undescribed deep-sea thyasirids.

Another potential suite of characters includes the nature of the energy substrate, the method of uptake of the substrate by the host, and the method of delivery to the bac-

terial symbionts. Lucinoideans appear to have specialized in symbioses involving reduced sulfur compounds (sulfide, thiosulfate, polythionate, or sulfite). Childress et al. (1986) identified methanotrophic bacteria (i.e., chemoheterotrophic, based on CH_4) in a symbiont relationship with a mytilid bivalve, broadening the spectrum of known chemosynthetic pathways in mollusks. Wood & Kelly (1989) isolated six different strains of methylotrophic (i.e., chemoheterotrophic, based on CH_3OH or CH_3NH_2) bacteria from the gills of both lucinids and thyasirids. Although they were unable to demonstrate that the bacteria were housed within the gills and were indeed symbiotic, the possibility of other novel metabolic pathways cannot be discounted at this time.

The site of uptake of sulfur compounds by the bivalve host is poorly understood. Three possibilities have been suggested: (1) the mantle cavity, with water entering either through the anterior inhalant current or through the pedal opening and uptake occurring directly by the gill (e.g., Reid & Brand, 1986); (2) the foot (e.g., Turner, 1985), with delivery by the blood; and (3) the gut, through removal of acid-labile reduced compounds bound to sediment (e.g., Reid & Brand, 1986). Accordingly, there are several alternative environmental sources or locations of sulfur compounds, including sediment pore water, water diffusing into the burrow, biogenic pockets of sulfide in the sediment, and grain coatings. If compounds are taken up by the foot, the host bivalve must have mechanisms for modulating internal sulfide concentration and toxicity levels, as through oxidation of sulfide to thiosulfate in the blood.

Several other potential character sources emerge from detailed studies of lucinid gills. The first is the presence of several different kinds of inclusions or granules. The presence of elemental sulfur is well documented from lucinid gill tissue, where it is present as globules. Vetter (1985) suggested that the sulfur sequestered by the bacteria of two lucinids functioned as an inorganic energy reserve in times of unavailability of external sulfide. Barnes (1992) maintained an intact symbiosis in *Codakia orbiculata* (Montagu, 1808), deprived of external reduced sulfur in the laboratory for more than 30 days. In addition to granules sequestering sulfur, Reid & Brand (1986) have assayed granules with high chromium, iron, and nickel content. The second is the presence of hemoglobin and possibly other transport proteins. The occurrence of "brown pigment granules," originally reported by Allen (1958), along with the reddish or pinkish color typical of many lucinid gills first led authors to suggest the presence of hemoglobin (Read, 1962; Jackson, 1973; Fisher & Hand, 1984). Hemoglobin was isolated and identified from *Myrtea spinifera* (Montagu, 1803) by Dando et al. (1985), who determined that it constitutes approximately 1% of the wet weight of the gill. Dando et al. (1985) suggest three possible functions for the hemoglobin: (1) it may act as a carrier of sulfide; (2) it may act as a store for oxygen during periods of closure of the inhalant tube while the animal is repo-

sitioning itself; or (3) it may act as a buffer to protect symbionts from oxygen interference with the anaerobic autotrophic process.

Finally, there is variation in the bioenergetics of translocation of fixed carbon products from symbiont to host. There is much indirect evidence for nutritional transfer (Southward, 1987; Fisher, 1990, and references therein), but few experimental studies documenting the nature of the transfer. Two primary modes of transfer are possible: (1) translocation of soluble organic compounds across the bacterial cell wall to the host, and (2) host digestion of the symbionts. Fisher & Childress (1986) document transfer of 40% of the carbon fixed by the bacterial symbionts of a solemyid bivalve to the host in soluble form, but little is known about the release of carbon compounds in lucinid bivalves (Distel & Felbeck, 1987). Evidence for host digestion of symbionts is poor for lucinids but good for thyasirids, where bacteria from the extracellular bacterial mass are endocytosed by the underlying cell membrane. Southward's (1986) illustrations of phagocytic vacuoles containing disintegrating bacteria are compelling, but this form of evidence does not address the dynamic question of nutritional energetics. Is phagocytosis and bacterial digestion a more primitive method of nutritional transfer than a relationship in which symbionts translocate soluble compounds to the host?

Estimates of the percentage of fixed carbon obtained from bacterial symbionts in lucinids range from at least half (Dando et al., 1986; Dando & Southward, 1986; Spiro et al., 1986) to much higher proportions (CoBabe, personal communication). The main form of evidence is the stable isotopic composition of host tissues. This is a very large topic, and the reader is referred to Fisher (1990) for discussion and a review of the literature. The point for purposes of systematics is that lucinids, by virtue of their symbionts, may range from partially to fully chemoautotrophic with respect to carbon and that the tightness of the symbiotic interaction is pertinent to the study of relationships.

It is possible that there has been coevolution of respiratory physiology in some host/symbiont pairs. Hentschel et al. (1993) have demonstrated that the symbiont of *Lucinoma aequizonata* (Stearns, 1890) respire nitrate rather than oxygen. The lucinid lives in a very low oxygen setting, and since it requires oxygen for its own respiration, nitrate respiration by the symbiont may be essential to survival.

Symbiont Systematics and Phylogeny

In spite of the fact that the bacterial symbionts have not been successfully cultivated, they have been extracted, purified, and identified. Phylogenetic analyses of the symbionts, based on 16S rRNA gene sequences, show that the symbionts fall within the unnamed gamma subdivision of the class Proteobacteria, a taxon described by Stackenbrandt et al. (1988) and which includes the purple photosynthetic bacteria and their allies. Symbiont trees (Distel

et al., 1988; Eisen et al., 1992) have a curious topology that does not correspond with current classification of the hosts, suggesting polyphyletic origins of bivalve chemosymbiotic relationships.

Traditional features of lucinid functional anatomy, new features derived from studies of chemosymbiotic relationships, and symbiont phylogenies all need to be incorporated and integrated with the shell characters that form the traditional basis for lucinid systematics.

Lucinid Systematics

Exterior and interior shell features are the bases for species descriptions, assignment of species to supraspecific taxa, and classification. The major revisions of the family are those of Dall (1901), Chavan (1937, 1938, 1969), and Bretsky (1971, 1976). Chavan's (1969) classification for the Treatise on Invertebrate Paleontology appeared in the same year that Sara Bretsky completed her doctoral dissertation, applying the methods of numerical taxonomy to produce one of the first phenetic classifications of a molluscan family. An additional systematic treatment of importance to this paper is Britton's (1972) revision of the supraspecific taxa allied with *Parvilucina*. All of these treatments are based on shell characters.

Bretsky (1971) used forty-two characters in her phenetic study, demonstrating that lucinid shell morphology alone can be used to generate large character sets. Her characters are almost all qualitative, and it would not be difficult to expand the shell data considerably by introduction of morphometric characters. Allen's (1958) comparative anatomical and functional data have not been translated into characters and used in lucinid systematics. Now there is a new wealth of ultrastructural and biochemical data, although unfortunately it has not been gathered in a comparative systematic context.

There are four major elements that are lacking in lucinid systematics, primarily because it has not caught up with the wealth of data generated by non-systematists. The first is the lack of incorporation of comparative anatomical and functional data into revisionary systematics. The second is the lack of incorporation of any of the new ultrastructural data and biochemical data bearing on lucinid chemosymbiosis. The third is the lack of clear diagnoses of taxa that would result from a cladistic approach that identifies clades using sets of shared derived characters. The fourth is the lack of quantitative approaches to shell morphology, and particularly to features of the hingeline.

The dilemma, from a systematic and evolutionary perspective, is how to use the wealth of new information most effectively. Should ecological, anatomical, functional, and ultrastructural data be used with shell morphology to generate phylogenetic hypotheses? Or are some of these data more valuable either in providing initial direction to research design or as overlays on phylogenetic hypotheses? A preliminary cladistic analysis of lucinoidean suprageneric taxa is in progress and will be published elsewhere.

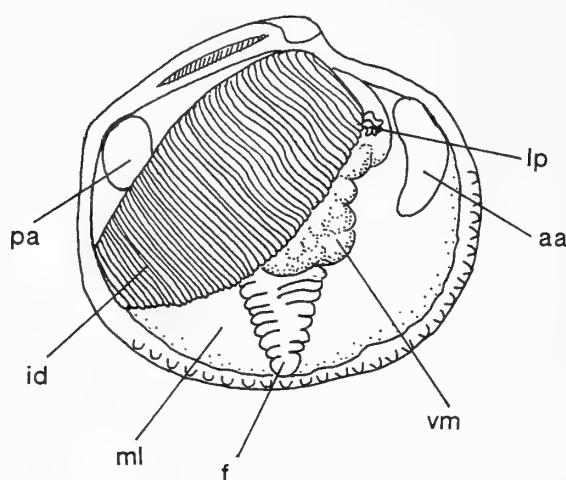


Figure 7

Parvilucina tenuisculpta. Right lateral view of the mantle cavity after removal of the right shell valve and right mantle lobe. aa, anterior adductor muscle; f, foot (only the vermiform portion is visible); id, inner demibranch; lp, labial papillae surrounding mouth (not normally visible from this perspective without moving ctenidium aside); ml, left mantle lobe; pa, posterior adductor muscle; vm, visceral mass. Based on specimens from UCMP loc. 11402 (60 m, Monterey Canyon).

In the case of the small-shelled lucinids, it is clear that genera and species must be better delineated before any of this new information will be useful. The following sections of this paper address the problem of *Parvilucina* in the eastern Pacific, laying the groundwork for analysis of chemosymbiotic species complexes.

SYSTEMATICS OF PARVILUCINA AND OTHER SMALL-SHELLED LUCINIDS

Dall (1901, p. 806) introduced *Parvilucina* to include a distinctive group of small to minute lucinids (<15 mm maximum shell length) with ovate, strongly inflated shells, weakly cancellate sculpture, and a full complement of hinge teeth. Dall (1901) and some subsequent authors (e.g., Chavan, 1937, 1938; Bretsky, 1971, 1976) have treated the taxon at subgeneric rank (under *Phacoides* Gray, 1847, *Linga* de Gregorio, 1884, or *Lucina* Bruguière, 1797). In the Treatise on Invertebrate Paleontology, Chavan (1969) elevated *Parvilucina* to generic rank and expanded the generic concept to embrace certain other groups of very small lucines at subgeneric rank, coordinate with *Parvilucina* s.s.; and Britton (1972) proposed an alternative scheme for classifying a different set of small-shelled lineages at subgeneric rank. Some subsequent authors (e.g., Jones & Thompson, 1984; Schweimanns & Felbeck, 1985; Reid & Brand, 1986) have used *Parvilucina* at generic rank without reference to subgenera, while others (e.g., Giere, 1985) have reverted to treating it as a subgenus of *Lucina*.

I am unconvinced that the small lucinids of either Chav-

an (1969) or Britton (1972) constitute a monophyletic group. It is not yet clear that the species that have been assigned to *Parvilucina* s.s. constitute a monophyletic group. In the systematic treatment that follows, *Parvilucina* s.s. is diagnosed by features of the type species. My first contact with the type species was through the observation of living specimens and subsequent dissections of fresh material.

INITIAL OBSERVATIONS OF THE TYPE SPECIES OF *PARVILUCINA*

Live specimens of *Parvilucina tenuisculpta* (Carpenter, 1864) were recovered from Smith-McIntyre Grab samples and epibenthic sled tows at 60 meters in the Monterey Canyon (60°50'N, 121°50'W). The substrate in this region is a blue-gray sandy to silty mud containing dead as well as live mollusks and abundant agglutinated worm tubes and agglutinated foraminifera. Bivalves dominate the mollusk fauna, and of the 10 most common bivalve species, three are lucinoideans: the lucinids *P. tenuisculpta*, and *Lucinoma annulata* (Reeve, 1850), and a thyasirid, *Axinopsida serricata* (Carpenter, 1864). All of the specimens of *P. tenuisculpta* are minute (<5 mm), in contrast to more typical populations from higher latitudes in which the largest shells commonly are 10–13 mm.

The most striking feature of the *Parvilucina* specimens is the deep, multilayered etching of the exterior of the shell (Figures 11, 12, 15, 16, 41, 42), which does not occur in any of the other bivalves at this station. Dall (1901) commented on the chalky shell of this species which "is almost invariably more or less abraded." Etching is definitely not a taphonomic feature of empty shells. It is equally well developed on live-collected material and is one of the features distinguishing this species from the other two minute-shelled species that occur off the west American coast.

A second feature that is conspicuous in the live specimens is an orange encrustation of the valves marking the position of the inhalant mucus tube. Allen (1958) noted a similar discoloration on lucinid shells, which he associated primarily with species that live in mud. When I placed live animals on sediment for observation, they made no attempt to burrow with the heel portion of the foot, although they did rapidly extend and withdraw the vermiform portion of the foot from time to time and appeared to be healthy. After 24 hours, one animal had moved to a position just below the sediment-water interface. Although these observations do not refute the possibility of a normal life position deep within the sediment, they at least suggest that the animal does not rapidly re-establish or assume such a position.

In mantle cavity dissection (Figure 7), the most conspicuous feature is the large, thick, brownish ctenidium, a single demibranch (left or right depending upon the perspective of the dissection). Individual elongate filaments are readily distinguished. The inhalant current is clearly anterior, and the general pattern of movement of carmine particles over the ctenidium is as in other lucinids. The

labial palps are not visible without manipulating the antero-ventral portion of the filaments aside to reveal minute, stubby palp vestiges. The mantle lobes are not fused along their anterior and antero-ventral margins. They are fused posteriorly to form a short, invertible exhalant siphon. An inhalant aperture was not observed, and documentation of the nature and extent of posterior mantle fusion and papillation of the middle mantle lobe in this species will require sectioning. The demibranchs are fused to the mangle edge posteriorly in the region of the exhalant siphon.

The other conspicuous features of the animal are the digestive gland, which is almost entirely covered by the ctenidia; the anterior and posterior adductor muscles; and the foot. The vermiform portion of the foot is highly wrinkled in the contracted state. The heel portion of the foot is concealed under the ctenidium and is well-developed and discrete. The features of the mantle cavity agree with those illustrated and discussed by Reid & Brand (1986) for material identified as *Parvilucina tenuisculpta*. Because their specimens were collected from Vancouver Island, British Columbia, the type area for the species, the identification is undoubtedly correct. It is the material from the southern California Borderlands (e.g., Jones & Thompson, 1984) that is more problematical because of the sympatry of *Parvilucina tenuisculpta* and *P. approximata* Dall, 1901, in this region. There are no observations to date of the animals of *P. approximata* or of the other eastern Pacific species with which it is also partly sympatric, *P. mazatlanica* (Carpenter, 1864).

The systematic treatment that follows provides: (1) criteria for recognition of the genus *Parvilucina*, s.s. based on the type species; and (2) new and preliminary criteria for separating the three eastern Pacific species. It is not a revision of the species complex, which will require further refinement and application of the criteria in a comprehensive study of material from the eastern Pacific. The geographic ranges listed require more precise endpoints based on full restudy of the complex.

The following abbreviations are used for repositories of specimens: CAS (California Academy of Sciences), UCMP (University of California Museum of Paleontology), USNM (United States National Museum of Natural History).

SYSTEMATIC TREATMENT

Class Bivalvia Linnaeus, 1758

Subclass Heterodonta Neumayr, 1844

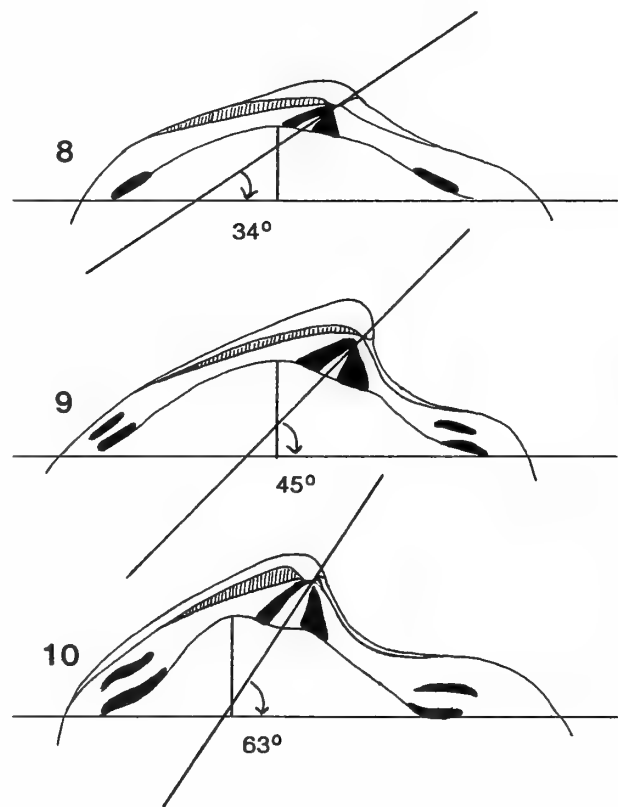
Superfamily LUCINOIDEA Fleming, 1828

Family LUCINIDAE Fleming, 1828

Subfamily LUCININAE Fleming, 1828

Genus *Parvilucina* Dall, 1901

Type species: *Lucina tenuisculpta* Carpenter, 1864, p. 643. By original designation.



Explanation of Figures 8 to 10

Comparative hinge morphology of three species of *Parvilucina*. 8. *P. tenuisculpta* (Carpenter), with the maximum hinge convexity farthest anterior and the lowest angle of cardinal inclination. 9. *P. approximata* (Dall), with an intermediate position of maximum hinge convexity and intermediate angle of cardinal inclination. 10. *P. mazatlanica* (Carpenter), with the farthest posterior position of maximum hinge convexity and highest angle of cardinal inclination.

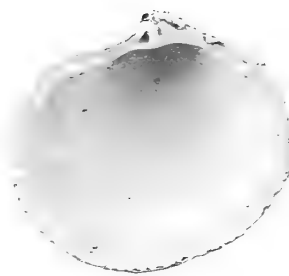
The genus *Parvilucina* is characterized by a combination of small shell size (<15 mm maximum length) and a shell shape in which length slightly exceeds height ($H/L = 0.92-0.94$); most of the shell length (and volume) is anterior to the beaks ($AL/L = 0.55-0.60$), and inflation is pronounced ($D/L = 0.59$) relative to most of the larger lucines ($D/L = 0.44$ in *Lucinoma annulata* Reeve). The interior margins of the shell valves are denticulate. The anterior and posterior dorsal areas range from undemarcated to well demarcated. Both concentric and radial sculpture are present, although the strength of radial sculpture is variable, and it may be developed most strongly along the anterior and posterior dorsal areas. The number of radial ribs can be used to characterize individual populations, but are not sufficient to identify specimens or to distinguish species. The lunule is clearly demarcated and asymmetric. It is characteristically somewhat longer, wider, and more deeply excavated on the left valve, and the right valve margin overlaps the left in a distinctive manner.



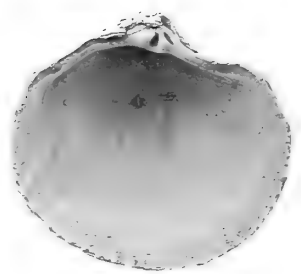
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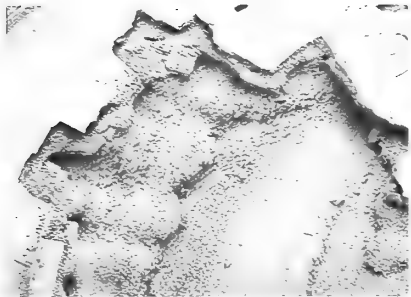
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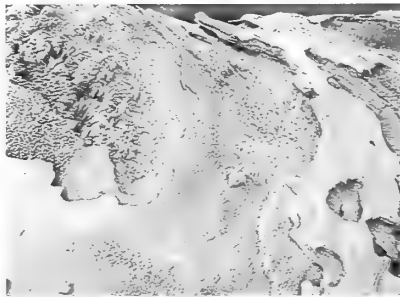
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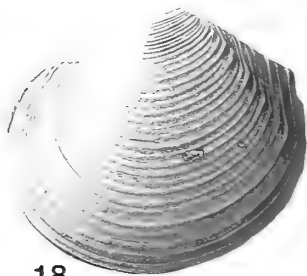
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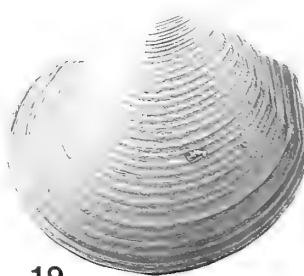
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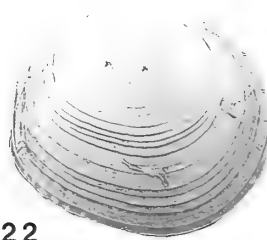
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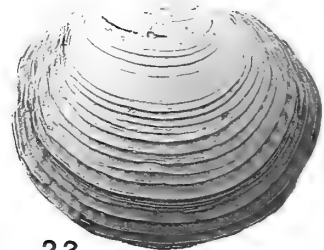
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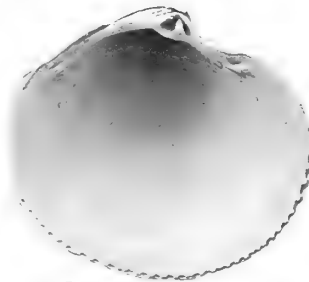
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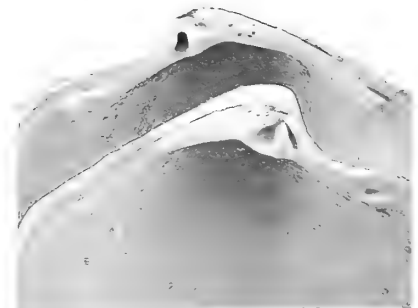
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26

that is most pronounced at the anterior end of the lunule. The ligament is opisthodontic, long, and narrow. The anterior muscle scar is short, broad, curved (relative to *Lucinoma* and most of the larger lucines), and contiguous with the pallial line. The smaller posterior adductor muscle scar is elliptical and is not contiguous with the pallial line. The lines of attachment of the ctenidia are faintly visible on the shell under appropriate lighting.

The hingeplate (Figure 8) has a full complement of teeth, with a pair (anterior and posterior) of double laterals in the left valve and a pair (anterior and posterior) of single laterals in the right valve. There are two cardinal teeth in each valve. The right posterior cardinal is bifid, and the right anterior cardinal is very poorly developed, especially in forms with a very deep lunule. Variation in the shape of the hinge plate and the orientation of the teeth seem to provide the most distinctive means for differentiating species in this group (Figures 8–10).

On shells of live-collected individuals, there is typically an orange discoloration of the shell where the anterior inhalant tube enters between the valves. The posterior exhalant siphon is inversible, as in other lucinids, but it is short and does not appear to be capable of extending to the sediment-water interface. The posterior portion of the mantle is unfused. In mantle-cavity dissection, the single ctenidial demibranch is thick, brownish in color, and so enlarged as to almost completely conceal the digestive gland. The labial palps are reduced to small, paired, dorsal and ventral lips surrounding the mouth. The second largest structure is the foot, which is divided into a heel portion and a vermiform portion that is strongly wrinkled in the contracted state. In living individuals, the foot may be extended in rapid thrusts to lengths exceeding the shell by four or five times.

Parvilucina tenuisculpta (Carpenter, 1864)

Figures 8, 11–17, 41–42

Original description: (as *Lucina tenuisculpta*) “Two living specimens of which one had the surface disintegrated.” [Carpenter, 1864, p. 602]. “S. Diego, living in 4 fm. (also

Puget Sound, *Kennerley*.) Var., dead in 120 fm. Cat. Is. (approaching *L. Mazatlanica*, Maz. Cat., no. 144).” [Carpenter, 1864, p. 611]. “Like *Mazatlanica*, Cat. 144, more convex, with finer sculpture. 4 fm. living, Cp. The island var. is intermediate. 120 fm. dead. CP.” [Carpenter, 1864, p. 642].

Carpenter (1865, p. 57) provided a more formal Latin description of the species, which is reproduced in Palmer (1958, p. 86–87).

Synonymy: Synonymies for this species are given by Grant & Gale (1931), Palmer (1958) Bretsky (1976), and Moore (1988). Bretsky (1976) tentatively included *P. approximata* and *P. mazatlanica* in the synonymy of *P. tenuisculpta*, and the identity of the 100 specimens that she included in her phenetic study is uncertain.

Type material and previous illustrations: Carpenter did not designate a type and cited material from three localities in the original description. The lectotype (designated as “holotype” by Palmer, 1958) is in the National Museum of Natural History (USNM 5244). The lectotype is figured by Bretsky (1976, pl. 27, figs. 11–13) and is from Vancouver Island, British Columbia. Dall (1901, pl. 50, fig. 5) was the first to illustrate the species. His drawing is of a specimen from Puget Sound, which he claimed to be the type locality, following Carpenter (1865). Figured hypotype material that agrees closely with the lectotype includes the specimens figured by Bretsky (1976, pl. 27, figs. 8–10) and the specimen figured by Britton (1972, fig. 5a).

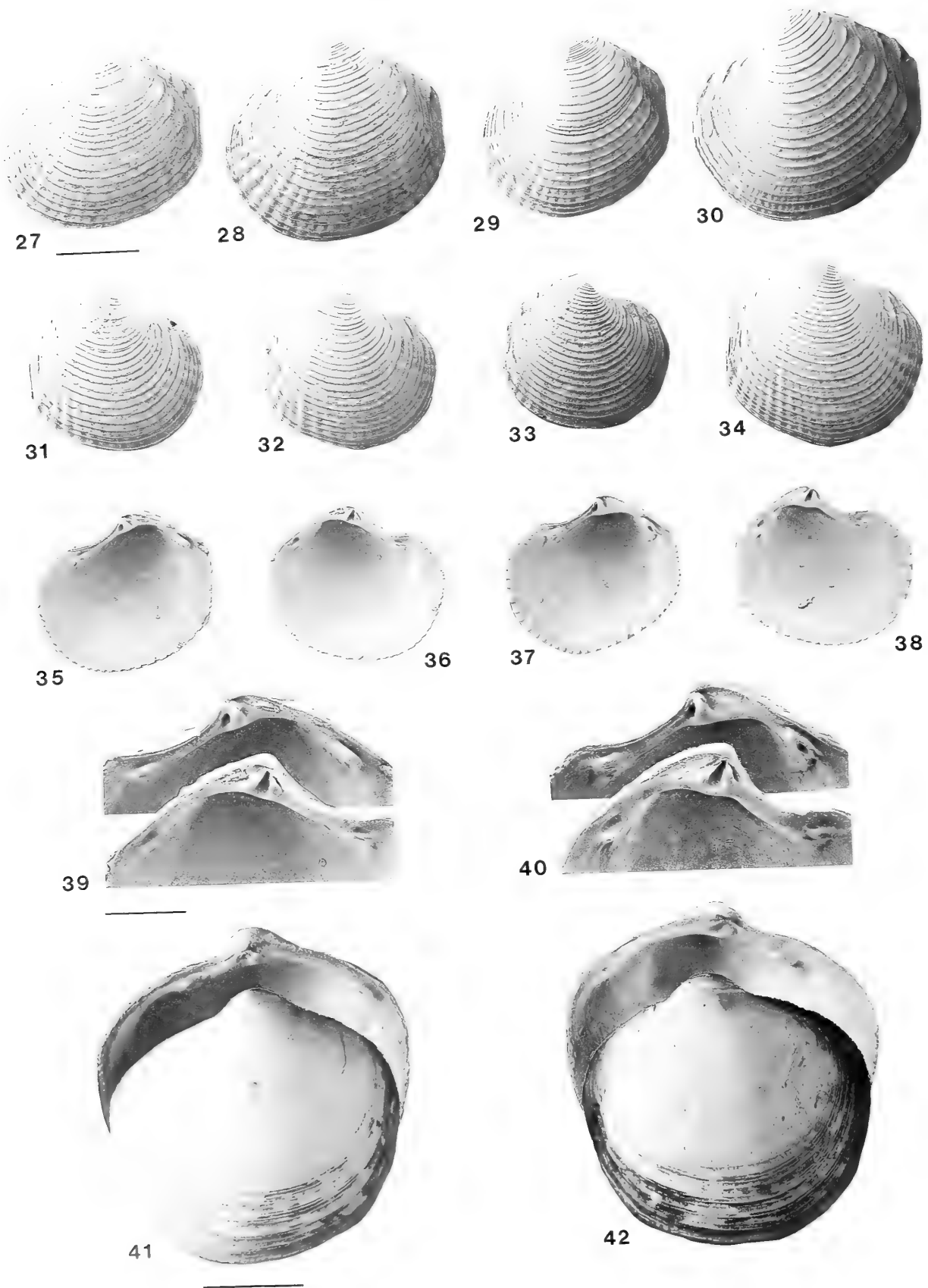
Figured specimens: The specimens figured herein are from 60 meters in Monterey Bay (UCMP 11402) (Figures 11–17) and “30–50 fathoms” in Edna Bay, Alaska (CAS 32429) (Figures 41–42).

Geographic range: Alaska to Baja California Sur. More precise endpoints of this range await restudy of the entire complex.

Stratigraphic range: Miocene–Holocene, central and southern California. Numerous reports of *Parvilucina tenuisculpta* from Miocene and younger rocks are summarized

Explanation of Figures 11 to 26

Scanning electron micrographs of the shells of *Parvilucina tenuisculpta* (Carpenter) from UCMP Loc. 11402, and *P. approximata* (Dall) from CAS Loc. 25610. 11–12. Exterior left and right valves of a live-collected specimen of *P. tenuisculpta* (UCMP 398616) Bar = 1 mm. 13–14. Interior right and left valves of a live-collected specimen of *P. tenuisculpta* (UCMP 398617) Bar = 1 mm. 15. Detail of multilayered etching on the valve illustrated in Figure 11. Bar = 200 μ . 16. Detail of multilayered etching on the valve illustrated in Figure 12. Bar = 200 μ . 17. Enlarged view of right (above) and left (below) hinges of the valves illustrated in Figures 13–14. Bar = 500 μ . 18. Exterior of isolated left valve of *P. approximata* (CAS 088315). Bar = 1 mm. (scale bar is the same for Figures 18–25) 19. Exterior of isolated left valve of *P. approximata* (CAS 088316). 20. Exterior of isolated left valve of *P. approximata* (CAS 088317). 21. Exterior of isolated right valve of *P. approximata* (CAS 088318). 22. Exterior of isolated right valve of *P. approximata* (CAS 088319). 23. Exterior of isolated right valve of *P. approximata* (CAS 088320). 24–25. Interior of paired right and left valves of *P. approximata* (CAS 088331). Bar = 1 mm. 26. Enlarged view of right (above) and left (below) hinges of valves illustrated in Figures 24–25. Bar = 500 μ .



by Moore (1988). These reports all require critical re-evaluation.

Habitat: Live-collected specimens are most common from 15 to 300 meters. The typical form of the species inhabits sulfide-rich fine silt or silty mud. I suspect that it lives shallowly buried within the anoxic (sulfide-generating) sediments that support chemosymbiosis, while maintaining contact with the sediment-water interface and an adequate level of oxygen to support aerobic metabolic function. The species is reported from a much broader range of habitats (Jones & Thompson, 1984), and it is therefore important to establish whether the populations morphologically distinguished herein as *P. approximata* and *P. mazatlanica* also differ in their ecology and function.

Supplementary description and diagnosis: *Parvilucina tenuisculpta* is uniquely distinguished from the other two eastern Pacific species by the following features: (1) multilayered etching of the shell that occurs while animals are alive (Figures 11–12, 15, 16, 41, 42); (2) larger maximum adult shell size (>10 mm); (3) relatively weak concentric sculpture that does not form sharp, well-defined, asymmetric (terraced) lamellae; (4) finer and weaker radial ribbing and correspondingly weak crenulation of the interior valve margins; (5) lack of demarcation of either the exterior anterior or posterior dorsal areas; (6) a shallower and broader lunule; (7) less well-developed lateral teeth; (8) a divergence angle of 56° between the cardinal teeth of the left valve; and (9) a relatively narrow, evenly arcuate hinge plate on which the cardinal teeth are set at a lower angle (34°) to the horizontal line connecting the laterals.

Remarks. The differences in hinge-plate morphology (cited above and illustrated in Figures 8–10) can be used to develop more formal morphometric criteria for distinguishing the three species. The shallowness of the lunule is not an artifact of etching of the shell. The lunule itself typically remains covered by a thin layer of periostracum and the details of lunule asymmetry are well preserved.

Parvilucina mazatlanica (Carpenter, 1857)

Figures 10, 27–40

Original description: Carpenter's (1857) original description, in Latin, is the first account of an eastern Pacific *Parvilucina*, and it does not contain information that distinguishes the taxon.

Synonymy: Grant & Gale (1931) recognized this as a valid species and provided a brief synonymy that includes references to its presence in the Pleistocene. Most frequently the name appears in synonymy with *Parvilucina tenuisculpta* (e.g., Bretsky, 1976). Abbott (1974) listed the name but did not characterize the species in his treatment of the North American species. Keen (1971) treated it as a distinct species, differentiated from *P. approximata* by its smaller size and relatively longer anterior end, based on her study of Carpenter's syntypes.

Type material and previous illustrations: The type lot of this species is in the British Museum. It was originally described by Carpenter (1857) as follows: "Tablet 472 contains the pair, and 14 valves of different ages." Carpenter's original camera lucida drawing remained unpublished until it was reproduced by Olsson (1961, pl. 31, fig. 3). It was reproduced again when the Paleontological Research Institution published Carpenter's 60 plates of the small-shelled species in the Mazatlán Collection (Brann, 1966, pl. 12, fig. 144). The best illustrations of the type lot, however, are the three drawings and two photographs of Keen (1968, pl. 56, figs. 29a, b; text figs. 5a–c).

Figured specimens: The specimens figured herein are from a large lot of fresh but mostly disarticulated shells from Puerto Escondido, Gulf of California (CAS 23805).

Geographic range: Gulf of California to Panama. More precise endpoints of this range await restudy of the entire species complex.

Explanations of Figures 27 to 42

Scanning electron micrographs of the shells of *Parvilucina mazatlanica* (Carpenter) from CAS Loc. 23805 and photographs of the shells of *P. tenuisculpta* (Carpenter) from CAS Loc. 32429. 27. Exterior of isolated left valve of *P. mazatlanica* (CAS 088321). Bar = 1 mm. (scale bar is the same for Figures 27–38). 28. Exterior of isolated left valve of *P. mazatlanica* (CAS 088322). 29. Exterior of isolated left valve of *P. mazatlanica* (CAS 088323). 30. Exterior of isolated left valve of *P. mazatlanica* (CAS 088324). 31. Exterior of isolated right valve of *P. mazatlanica* (CAS 088325). 32. Exterior of isolated right valve of *P. mazatlanica* (CAS 088326). 33. Exterior of isolated right valve of *P. mazatlanica* (CAS 088327). 34. Exterior of isolated right valve of *P. mazatlanica* (CAS 088328). 35–36. Interior of paired right and left valves of *P. mazatlanica* (CAS 088329). 37–38. Interior of paired right and left valves of *P. mazatlanica* (CAS 088330). 39. Enlarged view of right (above) and left (below) hinges of valves illustrated in Figures 35–36. Bar = 500 μ . (scale bar is the same for Figures 39–40). 40. Enlarged view of right (above) and left (below) hinges of valves illustrated in Figures 37–38. 41. Paired left (above) and right (below) valves of *P. tenuisculpta* (CAS 088332). Bar = 5 mm. 42. Paired right (above) and left (below) valves of the same specimen illustrated in Figure 41.

Stratigraphic range: Pleistocene to Holocene. The Pleistocene record is that of Jordan (1924) from Bahía Magdalena, and I have not examined the material.

Habitat: Unknown. Shells have been taken from 4 to 1024 meters (Keen, 1971), but none of the lots that I have examined can be associated with sulfide-rich sediments. Carpenter's syntypes were obtained from "shell washings" (sediment from crevices in larger bivalve shells, especially *Chama* and *Spondylus*). This species must be extremely abundant in some habitat, because individual lots may contain several thousand shells (e.g., CAS 23805). The valves appear fresh and unworn, always lacking the multilayered etching typical of *Parvilucina tenuisculpta*. Valves are commonly drilled (personal observation), a fact also noted by Carpenter (1857), who remarked of the 200 valves he examined, that "many of them (were) fresh from the banquets of carnivorous Gasteropoda."

Supplementary description and diagnosis: *Parvilucina mazatlanica* is uniquely distinguished from the other two eastern Pacific species by the following features: (1) a minute adult shell size (<5 mm); (2) a shorter, more strongly curved, anterior adductor muscle scar that is approximately equal in size to the posterior adductor scar; (3) a broad hinge plate that is the least evenly arcuate and on which the cardinal teeth are set at a high angle (63°) to the horizontal line connecting the lateral teeth; (4) a narrow divergence angle of 43° between the cardinal teeth of the left valve; (5) the most strongly developed hinge teeth, with two distinct anterior and posterior laterals in the left valve and a more prominently bifid posterior cardinal in the right valve.

Remarks: This species is more readily distinguished from *Parvilucina tenuisculpta* than from *P. approximata*. Both of the more southern species have sharp, asymmetric radial sculpture; and both species show a broad range of variation in the prominence of radial sculpture. There is almost always some well-developed radial sculpture in *P. mazatlanica*, whereas many specimens of *P. approximata* have only concentric lamellae (e.g., Figures 18, 19). In both species, radial ribs are broader and less numerous than in the type species. Both species show some degree of demarcation of the anterior and posterior dorsal areas. The posterior dorsal area is set off not only by an angulation of the concentric lamellae, but also by thickening of lamellae along the angulation. Lamellae are less frequently thickened along the demarcation of the anterior dorsal area.

Parvilucina mazatlanica is most readily distinguished from *P. approximata* by features of the hinge plate (Figures 9, 10).

Parvilucina approximata (Dall, 1901)

Figures 9, 18–26

Original description: "Shell small, tumid, nearly equilateral, white with a yellowish periostracum; beaks high,

full, with a rather emphatically depressed lanceolate lunule; sculpture of numerous fine, rounded, usually entire riblets separated by narrow sulci on the disk, but absent from the dorsal areas; concentric sculpture of low, feeble, distant, elevated lines which become feebly lamellose on the dorsal areas; hinge, especially the laterals, strong, normal; muscular scars as usual; basal margin conspicuously crenulate. Alt. 6.5, lon. 6.3, diam. 4.0 mm."

Dall (1901) considered this species to be consistently smaller (less than one-third the size) than *Parvilucina tenuisculpta* and to lack the chalky shell that he considered characteristic of *P. tenuisculpta*. He did, however, indicate that "very conservative persons" might wish to consider them extremes of a single polymorphic species. Dall made no reference to *P. mazatlanica*.

Synonymy: Synonymies for this species are given by Grant & Gale (1931) and Moore (1988), who included citations of fossil material. Grant & Gale (1931) treated it as a subspecies of *Parvilucina tenuisculpta*, and Bretsky (1976) included it tentatively in the synonymy of *P. tenuisculpta*. Keen (1971) and Abbott (1974) treat it as a distinct species.

Type material and previous illustrations: The Holotype is in the United States National Museum (USNM 96418), and the type area is the Gulf of California. Dall's drawing 1901, pl. 39, fig. 4) emphasizes the radial ribbing. Dall's original drawing has been reproduced by Keen (1971, fig. 274) and by Abbott (1974, fig. 5292), and there are no good photographic illustrations in the literature for the species. Pliocene hypotype material is figured by Durham (1950, pl. 18, figs. 12, 17) and Moore (1988, pl. 4, figs. 7, 8).

Figured specimens: The specimens figured herein are from a large lot from "30–58 fathoms" off the north side of Catalina Island, California (CAS 25610). Specimens in this lot, which includes some articulated individuals (Figures 35–40), are typical of the more northern populations of the California Borderlands. Individuals show less prominent radial ribbing here than in the Gulf of California and farther south.

Geographic range: Southern California (California Borderlands) to Panama. More precise endpoints of this range await restudy of the entire species complex. Longitudinal endpoints are less important than the distribution within the California Borderlands.

Stratigraphic range: Miocene? Pliocene–Holocene. I have reexamined Durham's Pliocene specimens (UCMP 32845–32848), which are well preserved and have the prominent radial ribbing typical of the more southern populations. Other reports require critical reevaluation.

Habitat: Shells have been collected intertidally (they are locally common in beach drift) to 1024 meters, but the precise habitat of this species is unknown. As in the case of *Parvilucina mazatlanica*, none of the lots that I have examined can be associated directly with sulfide-rich sed-

iments. Lots from the insular shelf of the Channel Islands (e.g., CAS 25610) represent an environment that is typically sediment-starved, coarser, higher in carbonate, and less rich in organic material. The holotype was collected "in 26 fathoms, sand." As in *P. mazatlanica*, valves consistently lack the multi-layered etching typical of *P. tenuisculpta*.

Supplementary description and diagnosis: *Parvilucina approximata* is distinguished from *P. tenuisculpta* by a shell that does not exceed 6 mm in adult size and does not develop multilayered etching of the exterior surface. It is further distinguished from both of the other eastern Pacific species by: (1) a moderately broad hinge plate with cardinal teeth set at an angle of 46° to the horizontal line connecting the lateral teeth; (2) a divergence angle of 59° between the cardinal teeth of the left valve (Figure 9).

Remarks: This species is least easy to diagnose because it is intermediate in many features although it is easily recognized by features of the hinge plate that invite more detailed morphometric documentation and comparison across species in the genus.

DISCUSSION AND CONCLUSIONS

The two inferences of sulfide-based chemoautotrophy in *Parvilucina tenuisculpta* are based on animals that came from sediments with high free sulfide. Reid & Brand (1986) analyzed specimens that were recovered from a fine silt with "a strong odor of hydrogen sulfide," and Felbeck et al. (1981) studied animals from a sewage outfall in the Los Angeles area, near White's Point, California. It is highly probable that both these reports do deal with the type species of *Parvilucina*: all of the material that I have seen from British Columbia and from sewage outfalls in southern California shows the same multilayered etching and hinge morphology. From my observations of live animals from the Monterey Canyon, I suspect that animals are not highly motile and that they live very shallowly buried with the shell positioned within highly reduced sediments that provide the energy source, obtaining oxygen and carbon dioxide directly from the overlying water. The multilayered etching of the shell may serve as an indicator of microhabitat chemistry and shell positioning.

In contrast, I suggest that the other two species of *Parvilucina*, (which consistently lack etching of the shell surface) may not be living with the shell positioned within reduced sediments, that the animals may be more active in their burrowing (consistent with more prominent sharp, asymmetric concentric sculpture that is stronger anteriorly and posteriorly). If they are substantially dependent upon chemoautotrophic bacteria, they may be using the foot to establish and probe galleries to locate tiny pockets of sulfide deeper within the sediment or to set up a system promoting the diffusion of H₂S from the reduced zone into the burrow system.

To understand the putative species complex in the eastern Pacific, it is essential that we have more information

about the environments and microhabitats that each species occupies and that we investigate and document the metabolism of each host species and the metabolic pathways of its bacteria separately. The active margin of the eastern Pacific provides a range of sedimentary settings with multiple sources of reduced sulfur (Kennicutt et al., 1989; Embley et al., 1990), and we have only begun to explore the full range of opportunities for organisms designed to live on the fringe between the world of molecular oxygen and the world of highly toxic, but deviously co-optable, reduced compounds.

ACKNOWLEDGMENTS

I am especially grateful to Paul Scott, Brian Morton, and Eugene Coan for the opportunity to participate in the bivalve workshop, to Jim Nybakken and the Moss Landing Marine Laboratories for their support, and to all of the workshop participants who were generous in sharing their expertise and observations of other elements of the bivalve community. I thank Kathleen Campbell and Emily CoBabe for stimulating discussions of bivalve chemosymbiosis and its geologic setting. Kathleen Campbell, Eugene Coan, and Emily CoBabe provided valuable critiques and suggestions for improvement of the manuscript. The scanning electron micrographs are the work of Geoff Avern of the Australian Museum. I thank Dave Lindberg (UCMP) and Bob VanSyoc (CAS) for facilitating the curation and deposition of specimens described and illustrated herein. This is contribution Number 1584 of the Museum of Paleontology, University of California, Berkeley, California.

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APPENDIX A

The vocabulary of chemosymbiosis contains a number of words that differ substantially in meaning while sharing some of the same Greek roots. I have used the term chemosymbiosis to refer to the general relationship; chemoautotrophy and chemoheterotrophy to distinguish the two main metabolic modes; and thiotrophy, methanotrophy, and methylophilic to distinguish three separate categories of compounds acting as energy sources. Other terms appear in the titles in the Literature Cited, making it difficult to search the chemosymbiosis literature. The following glossary is provided for systematists who are rusty on their biochemistry.

chemosymbiosis (adj. *chemosymbiotic*) A symbiosis (cooperative relationship) between a host species and bacterial (prokaryotic) species that synthesizes organic compounds from chemical sources in the environment. In the case of thiotrophic lucinoidean bivalves, the host provides a protected, anaerobic environment in (either extracellular or intracellular) within gill tissue and delivers CO_2 and reduced sulfur compounds. In return, the symbionts generate organic compounds that are transferred to the host. Chemosymbioses may involve either autotrophic or heterotrophic bacteria and may require an aerobic or an anaerobic environment.

chemosynthesis (adj. *chemosynthetic*) A metabolic pathway in which energy is obtained exclusively from chemical

compounds (i.e., not light; cf. *photosynthesis*). These compounds may originate deep within the earth's interior or may be of biogenic origin. Chemosynthetic bacteria do not require a host organism or symbiotic relationship.

chemoautotrophy. (adj. *chemoautotrophic*) A nutritional mode in which energy is obtained by oxidizing (i.e., breaking hydrogen bonds) reduced inorganic compounds (e.g., H_2S). For autotrophic nutrition, CO_2 is the only carbon source required. Strictly speaking, autotrophy refers only to the inorganic carbon source, and the term chemolithoautotrophy describes both the energy source and the carbon source. (cf. *chemolithotrophy*)

chemoheterotrophy. (adj. *chemoheterotrophic*) A nutritional mode in which both energy and carbon are obtained by oxidizing reduced organic compounds (e.g., CH_4). For heterotrophic nutrition a second carbon source is required.

chemolithotrophy. (adj. *chemolithotrophic*) Obtaining energy by oxidizing reduced inorganic compounds. In contrast to autotrophy, which refers to the carbon source, lithotrophy refers to the energy source. (cf. *chemoorganotrophy*)

chemoorganotrophy. (adj. *chemoorganotrophic*) Obtaining energy by oxidizing organic compounds. (cf. *chemolithotrophy*)

endosymbiotic. Refers to bacteria that are housed within the host, in this instance in specialized cells (*bacteriocytes*) within the gills. Endosymbiotic bacteria may be either intracellular or extracellular.

methylotrophic. Using CH_3 (Methanol or Methylamine) compounds in chemoheterotrophy.

methanotrophic. Using CH_4 (Methane) in chemoheterotrophy.

thiotrophic. Using one of a number of possible sulfur compounds (e.g., H_2S) in chemoautotrophy.

APPENDIX B

Potential characters and character states based on features of lucinoidean chemosymbioses that have been reported or hypothesized in the literature and discussed in the text. Some of the character states may not prove useful if it can be determined that they are ecologically varying and without a strong phylogenetic component. The list is not exhaustive and is intended as a preliminary step in bringing new data into a systematic framework.

1. Location and housing of bacterial symbionts
 - a. Extracellular (subcuticular, but external to underlying cell membranes)
 - b. Intracellular (in membrane-bounded vacuole within bacteriocyte cell) (characters 2-7 apply to taxa with intracellular bacteriocytes)
2. Size of bacteriocyte cells
3. Shape of bacteriocyte cells
4. Arrangement of bacteriocyte cells
 - a. Tubular stacking of bacteriocyte cylinders, with central hollow channels
 - b. Other arrangement
5. Lining of bacteriocyte channels, if present
 - a. Unlined
 - b. Lined by intercalary cells with dense microvillae
6. External surface of bacteriocyte cells
 - a. Smooth
 - b. With microvillae
7. Number of bacteria per membrane-bounded vesicle (vacuole) within bacteriocyte
 - a. One
 - b. Two
 - c. >10
8. Size of population of live bacteria maintained by host
 - a. Large
 - b. Small
9. Number of endosymbiont types
 - a. One
 - b. Two or more
10. Energy substrate
 - a. Reduced sulfur compounds
 - i. Sulfide
 - ii. Thiosulphate
 - iii. Polythionate
 - iv. Sulfite
 - v. Elemental sulfur
 - b. Other compounds (e.g. methane)?
11. Site of uptake of sulfur compounds by host
 - a. Mantle cavity: epidermis of the gill
 - b. Foot
 - c. Gut
12. Environmental source of reduced sulfur compounds (source is an initial rough proxy for source-specific adaptations)
 - a. Sediment pore water
 - b. Pockets of biogenic sulfide in sediment
 - c. Water diffused into burrow
 - d. Sediment grain coatings
13. Ability of host to modulate internal sulfide concentration and toxicity levels
 - a. Absent
 - b. Present, e.g., sulfide oxidized to thiosulfate in blood
14. Ability of bacterial symbionts to sequester sulfur as an inorganic energy reserve
 - a. Sulfur vesicles present
 - b. Sulfur vesicles absent
15. Evidence of phagosomes or phagocytic vacuoles within host cells
 - a. Present, with evidence endocytosis and digestion of bacteria
 - b. Absent
16. Presence of hemoglobin or other transport proteins in host blood
 - a. Present
 - b. Absent

17. Method of translocation
 - a. Evidence of soluble organics translocated across membranes
 - i. Present (compounds can be specified)
 - ii. Absent
 - b. Evidence of host digestion of symbionts
 - i. Phagosomes or phagocytic vacuoles present within host cells
 - ii. Phagosomes absent
18. Percentage of host nutritional needs met by nutritional transfer from symbionts

International Workshop on the Marine Bivalvia of California

A New Species of *Saxicavella*
(Bivalvia: Hiatellidae) from California with
Unique Brood Protection

by

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Abstract. A relatively common central and southern California infaunal bivalve species, *Saxicavella nybakkeni* Scott, sp. nov., is described. Significant siphonal, mantle, and reproductive differences between *Saxicavella* and other members of the Hiatellidae necessitate the erection of a new subfamily, **Saxicavellinae** Scott, subfam. nov.

INTRODUCTION

Small, infaunal bivalves composing the genus *Saxicavella* Fischer, 1878, have long presented vexing problems to malacologists. My introduction to the poorly understood genus *Saxicavella* came during a visit to the Natural History Museum of Los Angeles County (LACM) where I was shown several specimens of a new bivalve species from southern California that were tentatively placed in the genus *Paramya* Conrad, 1860 (Myidae). The shell was reminiscent of a very small *Panomya* Gray, 1857, but the animal lacked siphons.

I thought little about the LACM specimens until I received an inquiry from Michael Kellogg of the San Francisco Bureau of Water Pollution Control in 1989. He suggested the possibility of sexual dimorphism in *Saxicavella pacifica* Dall, 1916, based on specimens of *Saxicavella* obtained off San Francisco. Two forms had been sampled sympatrically, one elongate and slightly flaring, fitting Dall's original description of *S. pacifica*, and the other shorter and broadly flaring.

During sorting of live samples collected by epibenthic sled during the 1991 Moss Landing Marine Bivalve Workshop, several specimens of the LACM "*Paramya*" (which proved to be equivalent to Kellogg's short, broad *Saxicav-*

ella) were found. I seized the opportunity to study this perplexing bivalve, and was pleased to learn that it was especially hardy in laboratory conditions.

During subsequent discussions with Don Cadien of the Los Angeles County Sanitation District Marine Biology Laboratory and other members of the Southern California Association of Marine Invertebrate Taxonomists, I learned of *Saxicavella* specimens with possible external broods. Upon examination of these specimens I determined that two species of *Saxicavella* are present in California, and both utilize a previously unrecorded form of larval brood protection.

This paper erects a new subfamily for *Saxicavella*, provides additional information on the living animal, describes a new species of this genus from California, and documents a previously undescribed form of brood protection in bivalves.

MATERIALS AND METHODS

Seven live specimens of *Saxicavella* were collected off Moss Landing in Monterey Bay, California, by the R/V *Ricketts* at 31 m and 60 m depth using an epibenthic sled.

Individuals were live sorted from bulk sediment samples and maintained in running seawater at approximately 9°C for over 10 days with no sign of reduced activity. Live

specimens were placed in a glass dish of seawater and native sediments from the sample site. Crawling and burrowing activities were observed using a dissecting microscope. Active animals were also examined apart from the substrate, allowing a better view of the mantle, siphonal region, and foot.

In one specimen, the right valve and mantle were removed, and ciliary currents and organs of the mantle cavity were examined. Specimens were then relaxed for 18 hours in an isotonic solution of magnesium chloride and seawater (72 g MgCl_2/L). Following relaxation, specimens were fixed in 5% formalin and after two days transferred to 70% ethyl alcohol. Two specimens were prepared utilizing standard histological procedures at the Department of Zoology, University of Hong Kong, and were transverse sectioned at $6\mu\text{m}$. Alternate slides were stained with either Ehrlich's hematoxylin and eosin, or Masson's trichrome.

Abbreviations of institutions mentioned in the text: BMNH, The Natural History Museum, London; CAS, California Academy of Sciences, San Francisco; LACM, Natural History Museum of Los Angeles County, California; MCZ, Museum of Comparative Zoology, Harvard University, Massachusetts; MLML, Moss Landing Marine Laboratory, California; SBMNH, Santa Barbara Museum of Natural History, California; USNM, National Museum of Natural History, Washington, D.C.

SYSTEMATICS

Superfamily HIATELLOIDEA Gray, 1824

Family HIATELLIDAE Gray, 1824

[= SAXICAVIDAE Swainson, 1835]

Subfamily **Saxicavellinae** Scott, subfam. nov.

Type genus: *Saxicavella* Fischer, 1878.

Diagnosis: Shell less than 15 mm, thin, with only com-marginal striae; inequilateral, posterior end longer; hinge plate reduced, small posterior cardinal tubercle may be present in both valves; ligament posterior, very small, attached to a nymph. Siphons very reduced or absent, mantle fusion not complete ventrally (Type B of Yonge, 1957). The type genus is the only recognized member of this subfamily.

Yonge (1971) listed no less than six major differences between *Saxicavella* and other members of the Hiatellidae but continued to place it with other members of the family. The short or absent siphons, incomplete mantle fusion and heteromyarian condition provide ample characters to place *Saxicavella* into a new subfamily. Whereas *Hiatella*, *Panomya*, *Cyrtodaria*, and *Panope* have developed siphons, complete fusion of periostracal secreting surfaces of the inner surface of the outer mantle fold (Type C of Yonge, 1957), and are isomyarian, they are therefore retained in the subfamily Hiatellinae.

Saxicavella Fischer, 1878

Type species (monotypy): *Mytilus plicatus* Gmelin, 1791, ex Chemnitz MS, of Montagu, 1808 [ICZN Code Article 70c, deliberate misapplication of name], = *Saxicavella jeffreysi* Winckworth, 1930 [a new species based on Jeffreys, 1865:75–77, not a new name as stated].

Description: Shell small (<15 mm); elongate to rhomboidal; inequilateral, posterior longer; posterior end flaring, height of anterior end much less than posterior; slightly to widely gaping; pallial sinus absent. Hinge plate reduced, with only a sunken nymph posterior of beaks; cardinal teeth absent in adults. Siphons absent or greatly reduced, inhalant opening may have short lip.

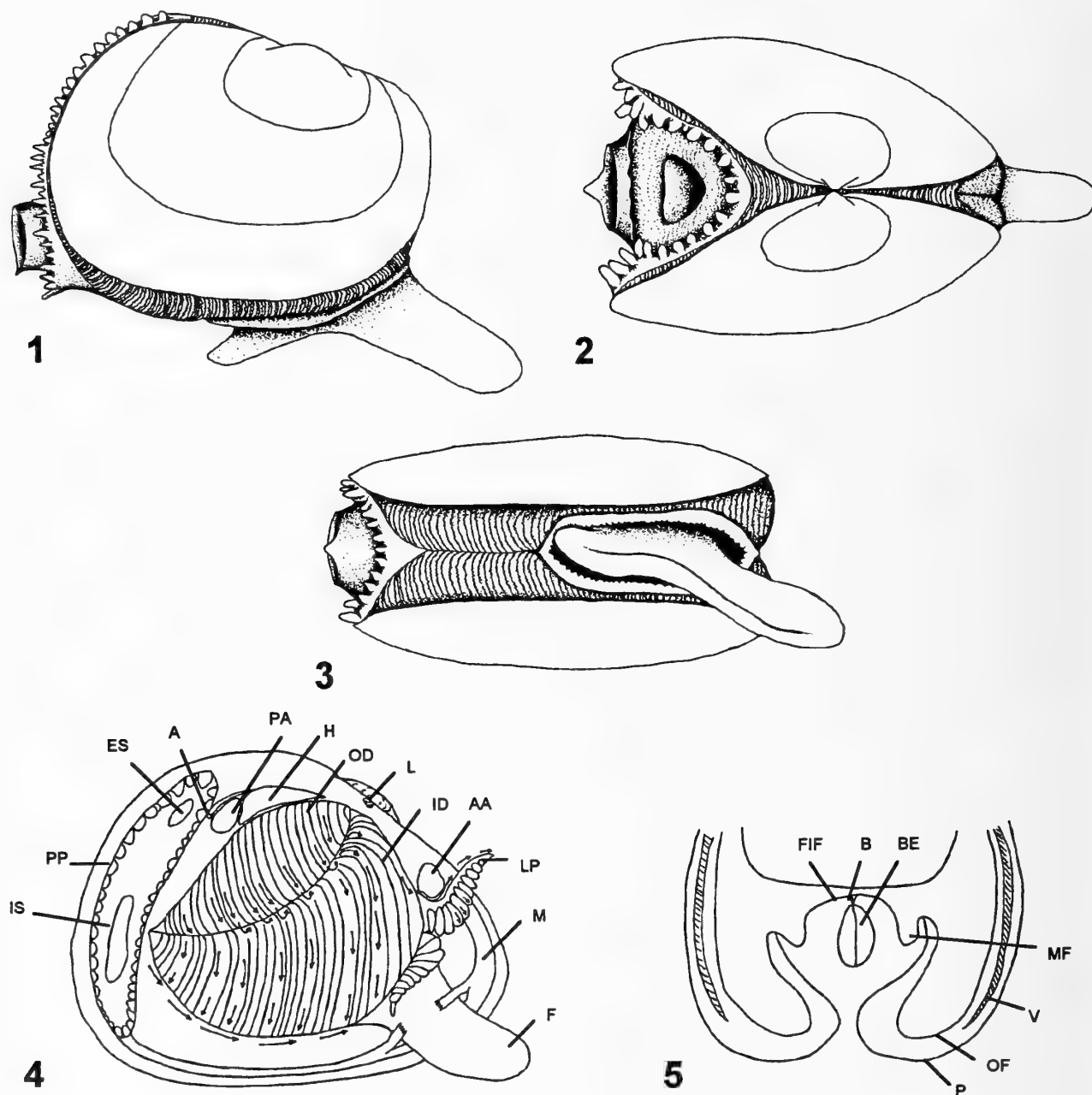
Discussion: Montagu (1808) first recorded and described a member of *Saxicavella* from the North Atlantic which he had been shown by J. Laskey and incorrectly assigned it to *Mytilus plicatus* "Chemnitz, 1785," from the Nicobar Islands, Bay of Bengal, India. Because Chemnitz (1785) is an unavailable work, this name is first made available in Gmelin, 1791, ex Chemnitz MS. Although Montagu did not include an illustration, his description of the shell adequately documents the small, broadly flaring species from Scotland and hinted that it might be a new species. Laskey (1811: pl. 8, fig. 2) provided an illustration of the specimen examined by Montagu.

Subsequent workers placed "*Mytilus plicatus*" of Montagu in widely separated families including the Hiatellidae (Turton, 1822), Psammobiidae (Jeffreys, 1847), Lyonsiidae (Gray, 1851), and Myidae (Weinkauff, 1866).

Forbes & Hanley (April 1848:149) extensively described and illustrated this species as juvenile *Saxicava rugosa* Linnaeus, 1767, but later stated in their appendix (Forbes & Hanley, 1852:248) that it was probably a new species. Jeffreys (1865) provided additional descriptions of "*Panope plicata* Montagu" and suggested possible synonyms that are now thought to belong in the Myidae and Corbulidae.

Fischer (1878) recognized the species as belonging to a distinct genus and erected *Saxicavella* for it. Lamy (1924) documented the details of the unstable placement of *S. plicata* (Montagu), but the type species of *Saxicavella* did not have a valid name until Winckworth (1930) proposed *S. jeffreysi*, some 122 years after Montagu's original description of the species.

As Winckworth did not designate a type specimen for *Saxicavella jeffreysi*, I hereby designate a **lectotype** from the Jeffreys collection in the U.S. National Museum of Natural History (USNM 171581, length = 9.0 mm, height = 4.9 mm, 1 right valve; Figure 6). The lectotype is a specimen figured by Jeffreys (1865, pl. 3, fig. 2, right specimen). Additional paralectotypes figured by Jeffreys are found in the following lots: USNM 878921 (Jeffreys 1865, pl. 3, fig. 2, left paired specimens) and USNM 171580 (Jeffreys, 1869, pl. 51, fig. 1). There was no precise locality associated with the Jeffreys material, but because



Explanation of Figures 1 to 5

Saxicavella nybakkeni Scott, sp. nov. Figures 1–3. Holotype in life (SBMNH 140090; length 5 mm; height, 3.5 mm; width, 4 mm). Figure 1. Lateral view as seen from the right side. Figure 2. Ventral view. Figure 3. Dorsal view. Figure 4. Organs and ciliary currents of the mantle cavity as seen from the right side with shell and mantle removed. Figure 5. Diagrammatic representation of a transverse section through the mantle, taken just posterior of the pedal gape. Key: A, anus; AA, anterior adductor muscle; B, byssus; BE, brooded embryo; ES, exhalant siphon; F, foot; FIF, fused inner mantle folds; H, heart; ID, inner demibranch; IS, inhalant siphon; L, ligament; LP, labial palp; M, mantle; MF, middle mantle fold; OD, outer demibranch; OF, outer mantle fold; P, periostracum; PA, posterior adductor muscle; PP, posterior papillae; R, rectum; V, valve.

he does mention a variety of locales around the British Isles, there is no doubt the specimens are from the northeast Atlantic Ocean.

Saxicavella nybakkeni Scott, spec. nov.

Figures 1–5

Description: Shell small (to 10 mm length, SBMNH 43802), thin, white, semi-transparent; rhomboidal, posterior end greatly expanded, anterior broadly rounded; inequilateral, posterior end much longer; surface uneven, rough, with uneven commarginal striae; valves widely gaping on all borders, only joined at beaks (width in life nearly equals length); beaks small, broad, not prominent; ligament small, not protruding, attached to small deeply sunken nymph just posterior of beaks; hinge plate narrow, without cardinal teeth.

Mantle thick, fleshy, expanded past shell margins in life, completely fused on all but ventral margin (Figures 1–3). Siphons very reduced; inhalant aperture with a very short, thin siphon with a sharply pointed ventral projection; exhalant siphon short, thick, dome-shaped with a narrow aperture. Posteriorly, stout papillae form a continuous lateral fringe along the shell margin.

Foot long, slender with short heel; byssal groove long, extending to the beginning of the heel. The organs and ciliary currents in mantle cavity are illustrated in Figure 4. Inner mantle folds and inner surface of middle mantle folds fused (Type B of Yonge, 1957; 156–157) except at pedal gape (Figure 5).

Type material: Holotype SBMNH 140090; dimensions, height–3.5 mm, length–5.0 mm; paratypes SBMNH 140091, plus others deposited at LACM, USNM, BMNH. All types preserved in 70% ethyl alcohol.

Type locality: United States, California, Monterey County, Monterey Bay, off Moss Landing; 36°48.7'N, 121°48.6'W; 31 m. Paratypes from 36°50.2'N, 121°51.7'W; 60 m.

Distribution: San Francisco (CAS) to Santa Monica Bay (SBMNH), California; 31–61 m.

Etymology: This species is named after Dr. James Nybakken of Moss Landing Marine Laboratory, who has consistently added to the knowledge of California marine mollusks and has motivated many students to pursue careers in malacology and marine biology.

Comparisons: The only other eastern Pacific species, *Saxicavella pacifica* (Figure 7), is more elongate and has a much smaller gape posteriorly than *S. nybakkeni*. *Saxicavella pacifica* also has a distinctly protruding ligament on a shallow nymph, compared to the small, non-protruding ligament of *S. nybakkeni* which is attached to a deeply sunken nymph.

The closest species to *Saxicavella nybakkeni* in external shell morphology is *S. sagrinata* Dall & Simpson, 1901, from the Caribbean (Figure 8). The external shell surface of this species has minute granules compared to the roughened, non-granular *S. nybakkeni*. *Saxicavella sagrinata* has narrow, pointed beaks, a small posterior cardinal tubercle, and a shallow nymph, unlike the broad beaks, lack of cardinals, and deeply projecting nymph in *S. nybakkeni*. The anatomy of the Caribbean species is unknown.

Living animal: When placed on its side in a petri dish with native soft sediment and cold seawater, the animal extends its foot down into the substrate and pulls itself vertically; the foot then immediately digs further into sediment and draws the animal further into the substrate. It is a very active crawler. The foot appears to produce a thick mucus that allows it to attach to substrate and obtain purchase. A very thin, clear byssus is also secreted.

While in an upright crawling position, the animal pushes the anterior end into the substrate, the foot then pulls anteriorly into the substrate while moving forward, forming a trough in the sediment. Maintaining a vertical orientation, the animal burrows forward into sediment (with valves opening and closing while burrowing) until only the posterior end is visible. The inhalant siphon is frequently covered with coarse sediment. The burrowing sequence in the laboratory, from horizontal to completely buried and at rest, took 4.5 minutes.

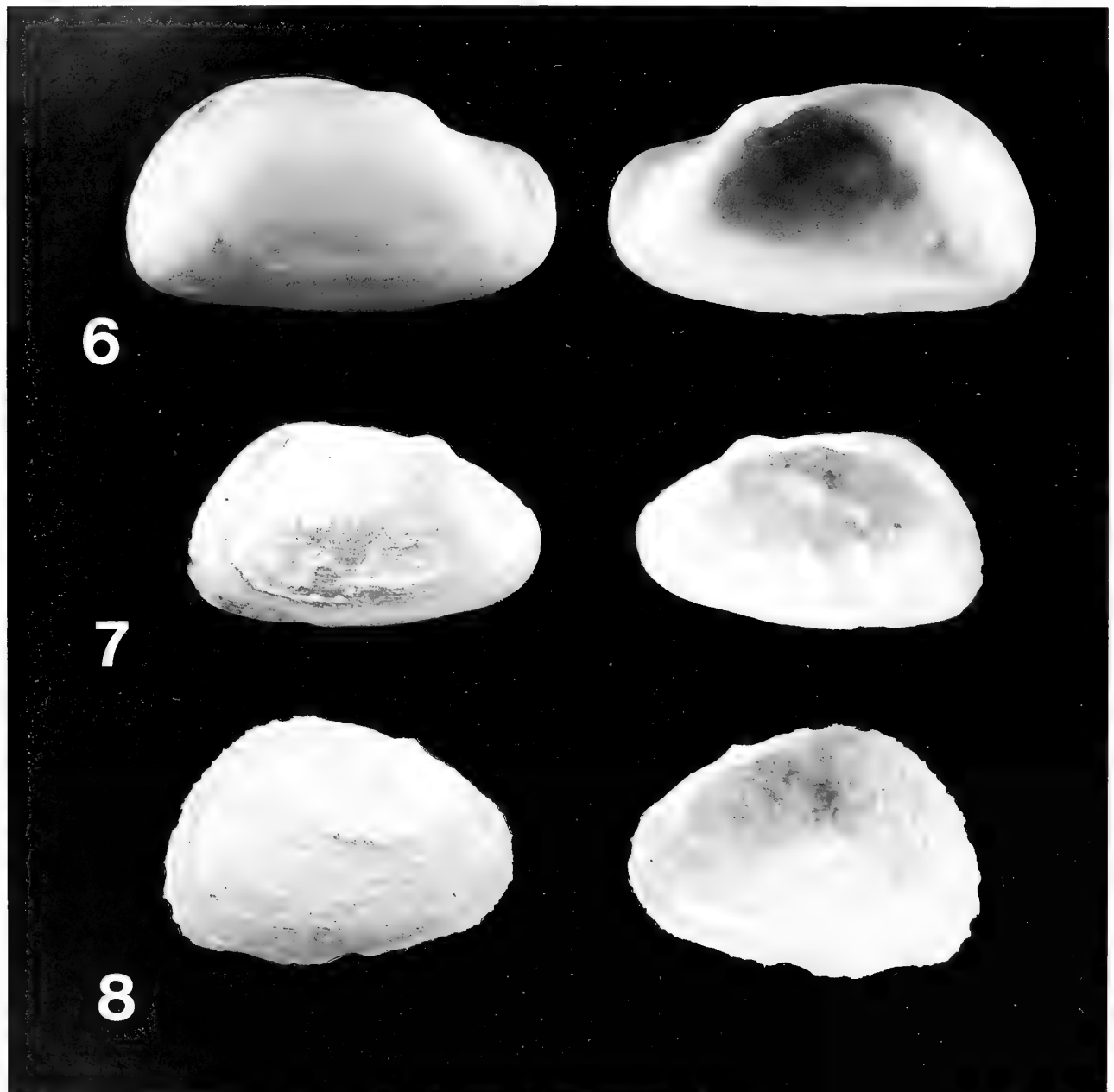
Reproductive Biology: Examination of histological sections has shown *Saxicavella nybakkeni* to be a simultaneous hermaphrodite that provides brood protection for its young. Embryos develop synchronously in a pouch posterior of the pedal gape. The pouch is formed between the fused inner mantle fold and the outer mantle fold (Figure 5). Embryos appear to be attached in the pouch by a byssus.

Brooding adults have been collected from April through July, but additional samples may show a longer or continuous breeding cycle. Up to 20 embryos have been found in a single brooding adult. Broods have not been detected inside the mantle cavity.

The method of embryo placement into the external brood pouch has not been discovered. It is highly probable, however, that the heel of the foot could easily provide a conduit from the mantle cavity, through the pedal gape to the external brood pouch.

DISCUSSION

Brood protection in bivalve mollusks is well documented and is found in more than 30 families (Sellmer, 1967; Mackie, 1984). The most common form of protection involves ovoviviparous incubation within the mantle cavity, generally within a suprabranchial chamber. Much less common is oviparous secondary brooding, whereby embryos are protected outside the parent. Two primary methods have been reported for secondary brooding: (1) initial incubation within the mantle cavity of the parent, with



Explanation of Figures 6 to 8

Figure 6. Lectotype **herein** of *Saxicavella jeffreysi* Winckworth, 1930; right valve (USNM 171581); length, 9.0 mm.

Figure 7. Holotype of *Saxicavella pacifica* Dall, 1916; right valve (USNM 209912); length, 5.5 mm.

Figure 8. Holotype of *Saxicavella sagrinata* Dall and Simpson, 1901; right valve (USNM 160063); length, 5.5 mm.

subsequent release and secondary incubation (often of dwarf males) external to the parent (Knudsen, 1961; Morton, 1972; Ó Foighil, 1985), and (2) by an invagination of the shell margin, as in the carditids *Milneria kelseyi* and *Thecalia concamerata* discussed by Yonge (1969).

In his description of the galeommatid, *Ephippodonta*

oedipus, Morton (1976) reported protection of two dwarf males in two external pouches made in the enlarged, reflected middle fold of the mantle. The dwarf males attach to the periostracum of the female while residing in a hole in the overlying mantle. In like manner, females of *Chlamydoconcha orcutii* Dall, 1884, provide a deep pore in the

mantle (presumably in the middle fold) for a single dwarf male to reside, and subsequently produce spermatozoa and fertilize the host female (Morton, 1981). In both species, fertilized eggs are internally incubated in the female ctenidia.

Saxicavella nybakkeni thus represents the first report of non-sexual brood protection between the outer and middle folds of the mantle. While embryos have not been located within the mantle cavity, it can be postulated that fertilization takes place within the parent followed by incubation to a byssus bearing stage. Larvae then travel to the external mantle pouch and are later released as crawl-away juveniles.

There have been no previous records of larval protection in the Hiatelloidea. With a reproductive mode well outside the hiatelloid line, as well as extreme siphonal reduction, it is possible that members of the Saxicavellinae should receive full family status.

ACKNOWLEDGMENTS

I would like to thank James Nybakken, Tracy Thomas and Steven Osborn of Moss Landing Marine Laboratories for enthusiastically assisting with the bivalve workshop. Brian Morton patiently taught me to draw these bivalves and clarified my understanding of their functional morphology and reproductive biology. The Department of Zoology at the University of Hong Kong supplied vital histological assistance. Laurie Marx touched up Figures 4 and 5. Pat LaFollette (LACM) shared specimens of the new species with me. Michael Kellogg first pointed out the California *Saxicavella* problem to me. Don Cadien and Tony Phillips loaned me wet preserved specimens with brooding larvae. Alan Kabat (USNM), Kenneth Boss and Silvard Kool (MCZ) assisted in solving the *Saxicavella* nomenclatural tangle and supplied important literature. Gene Coan provided continual support and advice on nomenclatural problems. Henry Chaney and Gene Coan reviewed early drafts of this manuscript. Funding to study the collections at the U.S. National Museum of Natural History was provided by the Smithsonian Institution Office of Fellowships and Grants.

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International Workshop on the Marine Bivalvia of California

Molluscan Evidence for a Late Pleistocene Sea Level Lowstand from Monterey Bay, Central California

by

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Abstract. One hundred and twenty-three molluscan taxa are reported from four samples collected from a sea level lowstand deposit located between 100 m and 300 m below sea level in Monterey Bay, central California. Ecological interpretations of these mollusks suggest temperatures essentially equivalent to those from Puget Sound, Washington, to southern British Columbia; much cooler water than exists in Monterey Bay today; and water depths of about 10 to 50 m. *Chlamys rubida* from these deposits yield a ^{14}C age determination of about 17,000 yr B. P. This age is generally equivalent to a worldwide sea level lowstand between 20,000 and 15,000 yr B. P. of at least 100 m below modern sea level. The cooler and shallow-water aspect of the lowstand molluscan fauna is in full accord with the late Pleistocene paleogeography of Monterey Bay.

INTRODUCTION

The presence of a late Pleistocene sea level lowstand deposit between 100 and 300 m below sea level in Monterey Bay is indicated by an assemblage of cool- and shallow-water mollusks dated at about 17,000 yr B. P. This molluscan fauna was collected by various individuals as grab and dredge samples over a period of about 20 years, and its cool-water nature was recognized since the beginning. However, the age of the fauna, first recognized by Powell & Chin (1984), resulted in a clearer understanding of what marine conditions in Monterey Bay were like during the last glacial cycle. This paper draws together the faunal ages, modern molluscan distributions and depth data, and paleoecological data from fossil marine vertebrates to give a better picture of conditions in Monterey Bay during the late Pleistocene.

The mollusks reported here were collected within greater Monterey Bay, between 100 and 300 m depth, and their positions are shown on Figure 1. Similar anomalous cool-water faunas have been recognized elsewhere in the Pacific. Eastern Pacific sites include the Revillagigedo Islands off central Mexico (Powell & McGann, unpublished data), Cordell Bank off central California (Powell et al., 1992), and off the coast of southern Oregon (Powell, unpublished data).

PREVIOUS STUDIES

Quaternary mollusks were first identified at depth in Monterey Bay during a sediment study by Yancey (1968) who recorded the extra-limital northern bivalve genus *Astarte* and suggests it might "be represented by Pleistocene shells that lived in Monterey Bay during a glacial period when marine temperatures were lower along the California coast." Addicott & Greene (1974) discussed the zoogeographic significance of a large number of *Astarte* dredged from southwest of Cypress Point (USGS loc. M5023) at a depth between 180 and 300 m. They indicated that these specimens should be "taken as evidence of climatic cooling associated with Wisconsin Glaciation" and strengthened this argument by citing the occurrence elsewhere in Monterey Bay of the 18,940 year old Northern Sea Cow, *Hydrodamalis gigas* (Zimmermann) (Jones 1967). Later, Greene (1977) discussed the cool- and shallow-water nature of two invertebrate collections (USGS locs. M4492 and M5023) from southern Monterey Bay; he found only three extra-limital northern taxa: *Astarte bennetti* (Dall) (= *Astarte* sp. here), *Bittium challisiae* Bartsch, and *Cryptonatica aleutica* (= *Natica clausa* (Broderip & Sowerby) here and not considered extra-limital here). I have reexamined Greene's (1977) collections; although the names of some taxa have changed, the collections still indicate a

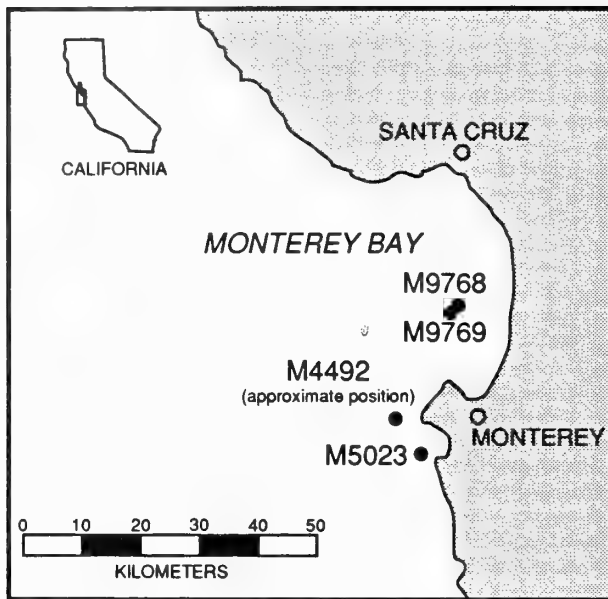


Figure 1

Index map showing the location of collection sites: M4492, M5023, M9768, M9769 in Monterey Bay, central California.

cool- and shallow-water environment. From two new grab samples, Powell & Chin (1984) described a fossil molluscan assemblage that suggested about the same conditions as occur today in Puget Sound, Washington, and dated *Chlamys rubida* (Hinds) from these deposits (J283-3) at $17,020 \pm 170$ yr B. P. (Powell & Chin, 1984; USGS-1830). The samples of Powell & Chin (1984) were further studied by Powell & McGann (1991), who identified benthic foraminifers and additional mollusks, all of which indicate the same cool-water conditions suggested previously by other authors.

PALEOECOLOGY

One hundred twenty-three molluscan taxa, 81 identified to specific level, are recognized from the four dredge and grab samples; these include four Polyplacophora, 53 Bivalvia, 64 Gastropoda, and two Scaphopoda (Table 1). Ecologically significant (i.e., outside depth range of the fossil locality or with a distributional endpoint within two degrees of the fossil locality) or unusual taxa are briefly noted (1) because of their use in the interpretation of this fauna as the first molluscan fossils from a submarine sea level lowstand deposit, and (2) because individual specimens are difficult or sometimes impossible to distinguish from modern specimens. Without radiometrically dating each specimen, it is sometimes impossible to distinguish the modern individuals from the fossil components of the assemblage.

Because of the small number of specimens and the poor quality of the depth data from the two deepest collection

sites (M4492, M5023), all four sites were combined for ecological interpretation. Although combining the sites could broaden the depth interpretations for the fauna, the small number of taxa from the two deep sites should serve to constrain the interpretation. Combining the data should not affect the temperature interpretation of the fauna and will hopefully give an accurate indication of the environment in which the fauna lived. Also by using a larger combined fauna, the modern contaminants will represent a smaller percentage of the entire fauna, and the temperature and depth determinations will be more representative of the fauna as a whole. It should be stressed that the ecological interpretations presented here are based on all the taxa recovered—none was omitted because it might be a modern contaminant.

Of the 123 molluscan taxa recorded in Table 1, 15% (18) are extra-limital northern taxa (Table 2) which, with one exception, do not today occur south of Washington state. The maximum overlap of the latitudinal range distributions of the taxa is between 48°N and 54°N (Figure 2), using range data from Bernard (1983) for the Bivalvia, from Keen (1937) and Burch (1944–46) for the Gastropoda, and from Abbott (1974) for the Polyplacophora. Cool-water extra-limital taxa (Table 2) and the maximum overlap of distributional ranges suggest much cooler water conditions than exist at the latitude of Monterey Bay today; these conditions are essentially equivalent to Puget Sound to southern British Columbia. If all the modern contaminants, recognized and unrecognized, were eliminated from this fauna, the remaining mollusks would probably indicate even cooler water temperatures. Seven taxa—*Semele venusta* (Reeve), *Antiplanes santarosana* (Dall), *Bittium interfossum* (Carpenter), *Bittium quadrifilatum* (Carpenter), "*Mangelia*" *philodice* (Dall), *Tegula aureotincta* Forbes, and *Turritella cooperi* Carpenter—are near the northern end of their modern range at Monterey Bay (36°N) and are therefore thought to be modern contaminants. Most of these taxa are only questionably assigned to species, and if material was available for precise identification, the number of these southern ranging taxa might be reduced.

The paleobathymetry inferred here is determined from depth data from Bernard (1983) for the Bivalvia and from various sources for the Gastropoda and Polyplacophora. The depth of deposition inferred from the mollusks is between about 10 m and 50 m, or within the inner part of the inner shelf zone. This depth range is much shallower than the 100 to 300 m depth from which these samples were collected. The depth of deposition indicated by the molluscan fauna is to be expected if the age of this fauna corresponds with the 20,000 to 15,000 yr old sea level minimum indicated by the radiometric age of these specimens reported by Powell & Chin (1984). During this sea level lowstand, sea level was at least 100 m below modern (Chappell, 1983). If the depth of this sea level lowstand is subtracted from the depth from which the samples were collected, it should indicate the depth at which the mollusks lived—in this case, between sea level and 200 m, a depth

Table 1

Pleistocene molluscan taxa from the sea level lowstand recorded about 17,000 yr B.P. in Monterey Bay, central California. [] = fragments.

Taxa	Localities				Comments
	M4492	M5023	M9768	M9769	
MOLLUSCA					
Polylacophora					
<i>Ichnochiton trifida</i> Carpenter, 1864	—	—	2	—	An extra-limital northern taxon; Abbott (1974) lists its range as "Alaska to Puget Sound, Washington." Identified by the late Antonio Ferreira.
<i>Mopalia</i> sp., cf. <i>M. ciliata</i> (Sowerby, 1840)	—	—	1	—	Abbott (1974) reports the range of this taxon from "Alaska to Monterey, California." Identified by the late Antonio Ferreira.
<i>Mopalia</i> sp., cf. <i>M. sinuata</i> Carpenter, 1864	—	—	1	1	Abbott (1974) reports the range of this taxon occurring from "Alaska to Monterey, California." Identified by the late Antonio Ferreira.
<i>Tonicella lineata</i> (Wood, 1815)	—	—	—	1	Identified by the late Antonio Ferreira.
Bivalvia					
<i>Acila</i> (<i>Truncacila</i>) <i>castrensis</i> (Hinds, 1843)	—	[1]	—	1	Represented by a single very small translucent upper valve. The small size of the specimen makes it questionably referable to this genus.
<i>Anomia</i> ? sp.	—	—	1	—	
<i>Astarte</i> sp.	—	60	—	4	This taxon was referred to <i>A. loxia</i> (Dall, 1903) by Addicott and Greene (1974), but there is some question about the type of <i>A. loxia</i> (Dall). Paul Scott (personal communication, 1991) refers it to <i>A. arc-tica</i> (Gray, 1824) based on similar and possibly overlapping morphologies. The genus is extra-limital and occurs as far south as Puget Sound, Washington (48°N) in the eastern Pacific.
<i>Axinopsida serricata</i> (Carpenter, 1864)	—	—	4	27	This specimen may represent the first fossil occurrence of this taxon.
<i>Cardiomya</i> sp., cf. <i>C. planetica</i> (Dall, 1908)	—	—	1	—	
<i>Cardiomya pectinata</i> (Carpenter, 1864)	—	—	—	9	Pieces of valves which show radial sculpture may be referable to either of the above taxa, but because of their incomplete nature cannot be identified with certainty.
<i>Chlamys hastata hericius</i> (Gould, 1850)	[1]	—	—	—	
<i>Chlamys rubida</i> (Hinds, 1845)	3[2]	—	5	10[14]	
<i>Chlamys</i> sp.	[10]	—	—	—	

Table 1
Continued.

Taxa	Localities				Comments
	M4492	M5023	M9768	M9769	
<i>Clinocardium blandum</i> (Gould, 1850)	—	—	[1]cf.	9[27]	This taxon is considered synonymous with <i>C. fucanum</i> Dall, 1907 (P. Scott, personal communication, 1991). Bernard (1983) cites the range of this taxon as from 48°N to 54°N.
<i>Clinocardium nuttallii</i> (Conrad, 1837)	1	—	—	—	This taxon is synonymous with <i>C. divaricata</i> (Orbigny, 1845) and <i>C. inflata</i> Carpenter, 1864 (Moore, 1983).
<i>Codakia (Epilucina) californica</i> (Conrad, 1837)	—	1	—	—	
<i>Compsomyx subdiaphana</i> (Carpenter, 1864)	—	—	1	1	
<i>Compsomyx</i> sp.	[2]	—	—	—	
<i>Crenella decussatus</i> (Montagu, 1808)	—	—	1	9	
<i>Cuspidaria</i> sp.	—	—	—	1	This is an extra-limital taxon whose modern range in the eastern Pacific is from the Bering Sea to Amchitka Island in the Aleutian Islands (52°N) (P. Scott, personal communication, 1991). This is the first fossil record for this taxon.
<i>Cyclocardia ovata</i> (Rjabinina, 1952)	2	—	—	—	
<i>Cyclocardia ventricosa</i> (Gould, 1850)	2	—	10[1]	2	The present specimens are identical to the elongate Recent form, <i>C. v. montereyensis</i> , described from Monterey Bay by Smith and Gordon (1948). Hertlein and Grant (1972) indicate that "... inspection of a large series of specimens of this subspecies reveals that there are forms which imperceptibly grade into typical <i>C. ventricosa</i> ."
<i>Cyclocardia</i> sp.	1	2[3]	—	[10]	This taxon is represented by fragments or extremely small valves which are not well enough preserved or large enough to assign to species.
<i>Delectopecten</i> sp., cf. <i>D. vancouverensis</i> (Whiteaves, 1893)	—	—	[3]	3[4]	<i>Glycymeris septentrionalis</i> (Middendorff) includes <i>G. barbarensis</i> of Arnold, 1903 (not of Conrad, 1857), <i>G. corteziana</i> Dall, 1916, <i>G. guadalupensis</i> Strong, 1938, <i>G. migueliana</i> Dall, 1916, <i>G. profunda</i> (Dall, 1878), and <i>G. subobsoleta</i> (Carpenter, 1864) (Powell, 1991).
<i>Glycymeris septentrionalis</i> (Middendorff, 1849)	—	49	—	—	
<i>Hiatella arctica</i> Linnaeus, 1758	—	—	—	16	

Table 1
Continued.

Taxa	Localities				Comments
	M4492	M5023	M9768	M9769	
<i>Hiatella?</i> sp.	[1]	—	—	—	One, moderately large, broken valve missing the hinge is too poorly preserved to assign to species.
<i>Lucinoma annulatum</i> (Reeve, 1850)	—	—	—	1	Coan (1971) gives the southernmost confirmed modern record for this taxon as the outer coast of Washington, with dubious specimens reported from San Pedro, and Point La Jolla, California. Considered an extra-limital northern taxon; individuals from the Monterey Bay lowstand are smaller than normal with a maximum width of only 23.6 mm.
<i>Macoma elimata</i> Dunnill and Coan, 1968	8[1]	—	—	15[15]	
<i>Macoma obliqua</i> (Sowerby, 1817)	—	—	—	13	
<i>Miodoniticus prolongatus</i> (Carpenter, 1864)	—	3	—	3	
<i>Modiolus</i> sp.	—	—	1	[8]	Because of their small size, maximum length of 14.9 mm length, these valves can only questionably be assigned to species. Bernard (1983) reports the occurrence of this taxa from 37°N to 49°N. It is a northern extra-limital taxon which today only occurs as far south as Neah Bay, Washington (47°N) (P. Scott, personal communication, 1991). The specimen referable to this taxon is represented by a single chondrophore.
<i>Musculus</i> sp.	—	—	[3]	[13]	
<i>Mya</i> sp., cf. <i>M. arenaria</i> Linnaeus, 1758	—	—	1	3[2]	
<i>Mya truncata</i> Linnaeus, 1758	—	—	—	1	
<i>Mya</i> sp.	—	—	—	[1]	Bernard (1979) states that records of this taxon south of the Bering Sea should be assigned to <i>N. permula</i> (Müller, 1779), making this another extra-limital northern taxon. This is another extra-limital taxon, which does not occur south of the Pribilof Islands (61°N) in the Bering Sea today (Scott, personal communication, 1991).
<i>Mytilus</i> sp.	—	[10]	—	—	
<i>Nemocardium centiflosum</i> (Carpenter, 1864)	—	1	[1]	2	
<i>Nuculana minuta</i> (Fabricius, 1776)	—	—	—	1	
<i>Nuculana radiata</i> (Krause, 1885)	—	—	1	—	<i>Pandora</i> sp. <i>Parvilucina tenuisculpta</i> (Carpenter, 1864)
	—	—	[1]	—	
	—	—	9	2	

Table 1
Continued.

Taxa	Localities				Comments
	M4492	M5023	M9768	M9769	
<i>Patinopecten caurinus</i> Gould, 1850	[2]	1	—	—	This species has several subspecific names. The form found in these deposits is <i>P. s. ruderata</i> (Deshayes, 1853) which is an ecological morphotype usually associated with empty pholadid burrows.
<i>Philobrya setosa</i> (Carpenter, 1864)	—	[2]	—	2	
<i>Pododesmus?</i> sp.	—	—	1	—	
<i>Protothaca staminea</i> (Conrad, 1837)	—	—	—	1[2]	
<i>Protothaca</i> sp.	—	—	1	—	Specimens from Monterey Bay agree with Dall's description of this taxon but some are larger than commonly encountered, obtaining a maximum length of 12 mm, and so are questionably referred to this species.
<i>Psephidia</i> sp., cf. <i>P. ovalis</i> Dall, 1902	6	—	36	110	
<i>Semele venusta</i> (Reeve, 1853)	—	1	—	—	Coan (1988) reports the northern occurrence of this taxon as Monterey Bay, California (latitude 36°38'N) but empty valves have been found from moderately deep water at Cordell Bank (latitude 38°00'N), about 110 km north of its cited range. Because of the southern range of this taxon, the single valve reported here is probably a recent contaminant and not part of the fossil fauna.
<i>Serripes</i> sp.	—	—	—	1	Considered an extra-limital taxon as the two species of this genus in the northeastern Pacific, <i>S. groenlandicus</i> (Bruguère, 1789) and <i>S. laparousii</i> (Deshayes, 1839), occur no further south than Willapa Bay, Washington (47°N) (P. Scott, personal communication, 1991).
<i>Solen</i> sp.	—	—	—	[1]	All specimens show color and one pair of valves contains dried animal tissue indicating that it is a modern contaminant to the fossil assemblage. The other valves may be fossil.
<i>Spisula?</i> sp.	—	[1]	—	—	
<i>Tellina</i> (<i>Morella</i>) <i>carpenteri</i> Dall, 1900	2	—	1	3	
<i>Tellina</i> sp., cf. <i>T. (Angulus) nuculoides</i> (Reeve, 1854)	—	—	1	7	These well-preserved valves are only questionably referred to this taxon as they

Table 1
Continued.

Taxa	Localities				Comments
	M4492	M5023	M9768	M9769	
<i>Thracia myopsis</i> Möller, 1842	—		1[2]	[1]	are smoother and have a slightly more truncate posterior end than specimens illustrated by Coan (1971). Coan (1990) reports the modern occurrence of this taxon in the eastern Pacific as "... the Arctic coast to Alaska, the Bering Sea and Aleutian Islands, south to ... British Columbia. However, there is a single, small right valve from off Point Loma, California!" Since the specimens reported here are outside the normal modern range of this species, it is considered extra-limital.
<i>Thyasira gouldii</i> Philippi, 1845	—	—	4	8	This is another extra-limital northern taxon whose modern range is from Prince William Sound, Alaska to Malcolm Island, British Columbia (51°N) (Scott, personal communication, 1991), although Smith and Gordon (1948) report a single living individual from Monterey Bay.
<i>Yoldia (Cnesterium) seminuda</i> Dall, 1871	—		[1]cf.	1	
Gastropoda					
<i>Acteocina culcitella</i> (Gould, 1852)	—	—	5	3	The southern geographic limit of this taxon is Monterey Bay.
<i>Acteocina eximia</i> (Baird, 1863)	1		—	—	
<i>Admete coulthouyi</i> (Jay, 1839)	4	—	—	1	Similar to the above taxon, these specimens are poorly preserved and are not assigned to species.
<i>Amphissa columbiana</i> Dall, 1916	1		[1]cf.	37	
<i>Amphissa</i> sp.	—	[1]	—	?	Identified by Ronald Shimek. A single shell of this species was collected at Point Sur by Dall (Smith and Gordon, 1948) but was lost when they examined the Monterey Bay fauna. Identified by Ronald Shimek.
<i>Antiplanes</i> sp.	2	—	1	1	Bartsch (1917) reports the modern occurrence from the San Juan Islands, British Columbia making this another extra-limital northern taxon.
<i>Antiplanes (Rectiplanes)</i> sp., cf. <i>A. santarosana</i> (Dall, 1902)	2		1	1	
<i>Astrea</i> sp., cf. <i>A. (Pomaulax) gibberosa</i> (Dillwyn, 1817)	[3]		—	—	
<i>Balcis</i> sp.	—		[2]	—	
<i>Bititium</i> sp., cf. <i>B. attenuatum</i> Carpenter, 1864	1	—	—	—	
<i>Bititium</i> sp., cf. <i>B. challsae</i> Bartsch, 1917	1	1	—	3[8]	

Table 1
Continued.

Taxa	Localities					Comments
	M4492	M5023	M9768	M9769		
<i>Bititium eschrichtii montereyense</i> Bartsch, 1911	1	—	—	1		McLean (1978) reports its range as from "Monterey Bay, California to San Martin Island, northern Baja California." Because this is a southern ranging taxon, it is interpreted as a modern contaminant.
<i>Bititium interfossum</i> (Carpenter, 1864)	1	—	16	—		
<i>Bititium</i> sp., cf. <i>B. quadrifidatum</i> (Carpenter, 1864)	1	—	—	—		
<i>Bititium</i> sp.	—	—	—	1		Another northern extra-limital taxon as Keen (1937) reports this species from latitude 48°N to 56°N.
<i>Boreotrophon</i> ? sp.	—	—	1	—		
<i>Buccinum</i> sp.	1	—	1	—		
<i>Calliostoma</i> sp.	—	1	—	—		
<i>Calyptraea fastigiata</i> Gould, 1846	[1]	—	2	10[4]		
<i>Clio</i> sp.	—	—	—	1		Identified by Ronald Shimek. Its small size and slightly worn condition make it impossible to identify accurately. Identified by Ronald Shimek.
<i>Crepidatella lingulata</i> (Gould, 1846)	—	—	—	2		
<i>Cylichna attonsa</i> (Carpenter, 1884)	—	—	4	1		
<i>Cylichna</i> sp.	—	—	4	—		
<i>Diodora</i> ? sp.	—	[1]	—	—		
<i>Exilodea</i> ? sp.	1	—	—	2		
<i>Fusinus</i> ? sp.	—	—	—	—		
<i>Fusitriton oregonensis</i> (Redfield, 1846)	—	—	1[2]	5[2]		
<i>Homalopoma</i> sp., cf. <i>H. lurida</i> (Dall, 1885)	—	—	—	3		
<i>Kurtziella</i> sp., cf. <i>K. plumbea</i> (Hinds, 1843)	—	—	—	1		
<i>Kurtziella</i> ? sp.	—	—	—	1		Identified by Ronald Shimek.
<i>Lirularia</i> sp.	—	—	1	1		
<i>Littorina</i> ? sp.	—	—	—	1		
<i>Lischkeia</i> (<i>Cidarina</i>) <i>cidaris</i> (Carpenter, 1864)	—	—	—	1		Identified by Ronald Shimek.
" <i>Mangelia</i> " <i>philodice</i> (Dall, 1919)	—	—	2	1		
<i>Margarites</i> sp.	—	—	1	1		
<i>Mitrella tuberosa</i> (Carpenter, 1965)	—	—	14	27		Lowstand specimens represent <i>N. m. indispuitabilis</i> Oldroyd, 1927 in that the axial ribs become obsolete on the body whorl.
<i>Muricid</i> indet.	—	—	[1]	—		
<i>Nassarius</i> (<i>Demonidia</i>) <i>mendicus</i> (Gould, 1849)	—	—	3	2		
<i>Nassarius</i> sp.	—	—	—	[1]		This taxon is represented by a single outer lip fragment which is reminiscent of <i>N. insculptus</i> (Carpenter, 1864).

Table 1
Continued.

Taxa	Localities				Comments
	M4492	M5023	M9768	M9769	
<i>Naica</i> (<i>Cryptonatica</i>) <i>clausa</i> (Broderip & Sowerby, 1829)	2	[1]cf.	1[1]	13[1]	Identified by Helen DuShane. Identified by Helen DuShane.
<i>Nitidiscala catalinae</i> (Dall, 1908)	—	—	—	1[2]	
<i>Nitidiscala sawinae</i> (Dall, 1908)	—	—	4[4]	—	
<i>Ocenebra interfossa</i> Carpenter, 1864	—	—	—	2	
<i>Odostoma</i> sp.	—	—	1	2	
<i>Oenopota</i> sp., cf. <i>O. bicarinata</i> (Couthouy, 1838)	—	—	—	1	An extra-limital northern taxon. Abbott (1974) reports its occurrence in the eastern Pacific from "Arctic Seas to Chirikoff Island, Alaska." But Burch (1944-1946) reports its range as Icy Cape, Arctic Ocean to Puget Sound. I have chosen to use Burch's range data. Identified by Ronald Shimek.
<i>Oenopota turricula</i> (Montagu, 1803)	—	—	4	—	
<i>Olivella baetica</i> Carpenter, 1864	—	—	2	13	
<i>Polinices pallidus</i> (Broderip & Sowerby, 1829)	—	—	—	1	
<i>Puncturella cucullata</i> (Gould, 1846)	—	—	—	5	
<i>Puncturella multistriata</i> Dall, 1914	—	—	—	1	An extra-limital northern taxon that ranges "... south to the Aleutians." (Abbott, 1974).
<i>Puncturella noachina</i> (Linnaeus, 1771)	—	—	3	4	
<i>Serpulorbis</i> ? sp.	[1]	—	—	—	
<i>Solariella</i> (<i>Minolia</i>) <i>permabilis</i> Carpenter, 1864	[1]cf.	—	—	1	
<i>Solariella</i> (<i>Machaeroplax</i>) <i>varicosa</i> (Mighels & Adams, 1842)	1	—	—	—	
<i>Solariella</i> sp.	2	—	2	1	A single smooth fragment of the body whorl which may be referable to either <i>T. montereyi</i> (Kiener) or <i>T. pulligo</i> (Gmelin). This taxon is extra-limital occurring from off the coast of Oregon north to the Bering Sea (Burch, 1945).
<i>Tegula</i> sp., cf. <i>T. aureotincta</i> Forbes, 1850	—	[1]	—	—	
<i>Tegula</i> sp.	—	[1]	—	—	
<i>Trichotropis cancellata</i> (Hinds, 1843)	—	—	3	5	
Trochid indet.	—	—	1	—	
<i>Trophonopsis fleenerensis</i> (Martin, 1914)	—	—	2	5	The modern geographic range of this taxon is not well known, but it occurs from at

Table 1
Continued.

Taxa	Localities				Comments
	M4492	M5023	M9768	M9769	
<i>Trophonopsis lasius</i> (Dall, 1919)	—	—	1	—	least Monterey Bay north to Humboldt County, California.
<i>Trophonopsis</i> sp.	—	—	—	1	This genus is represented by two distinct species from the Monterey Bay lowstand. This is another species which is believed to be a modern contaminant because of its southward ranging distribution, Monterey Bay, California to Cerros Island, central Baja California (Burch, 1944–1946).
<i>Turbonilla</i> sp.	—	—	—	3	
<i>Turritella caeperi</i> Carpenter, 1864	—	—	—	1	
<i>Turritella</i> sp.	—	—	—	—	
Scaphopoda					
<i>Cadulus</i> sp.	—	—	—	1	
<i>Dentalium pretiosum</i> Sowerby, 1860	—	3(cf)	2	—	

Table 2

Extra-limital northern taxa recovered from Monterey Bay sea level lowstand deposits.

Bivalvia

Astarte sp.
Clinocardium blandum
Cyclocardia ovata
Macoma obliqua
Mya sp., cf. *M. arenaria*
Mya truncata
Nuculana minuta
Nuculana radiata
Serripes sp.
Thracia myopsis
Yoldia seminuda

Gastropoda

Bittium sp., cf. *B. challsiae*
Kurtziella sp., cf. *K. plumbea*
Oenopota sp., cf. *O. bicarinata*
O. turricula
Puncturella noachina
Trichotropis cancellata

Amphineura

Ischnochiton trifida

range which is in agreement with the more specifically determined depth from the mollusks above (10 to 50 m).

Sixty-four species of benthic foraminifers and 9 species of planktic foraminifers were collected from two of the sites (Powell & McGann, 1991; M9768, M9769). These samples consist of similar quantities of inner shelf (0–50 m) and outer shelf (50–150 m) benthic foraminifers. The abundant inner shelf benthic foraminifers again suggest shallower water than the actual depth at which the fauna was collected.

In addition to the mollusks and foraminifers, skulls of two walrus [*Odobenus rosmarus* (Linnaeus)] (C. Repenning, personal communication, 1984; A. Bailly, personal communication, 1987) were recovered from the sea floor by fishing boats from an area extending from Cordell Bank off Point Reyes, Marin County to the northern part of Monterey Bay. Also, the partial skull of a Steller's Sea Cow (*Hydrodamalis gigas* (Zimmermann)) was dredged from the sea floor between Point Sur and Santa Cruz just north of Monterey Bay (Jones, 1967) and dated at about 19,000 yr B. P. The modern distribution of *Odobenus rosmarus* (Linnaeus) is Arctic, from Aleutian Islands in the Pacific Ocean north to Arctic seas. *Hydrodamalis gigas* (Zimmermann) is now extinct, but its previous habitat was in the Commander Islands, southwest Bering Sea (55°N).

These marine mammal fossils also suggest cooler water conditions along the coast of central California during the late Pleistocene than exist today and suggest much cooler water conditions than those indicated by either the mollusks or the foraminifers. The discrepancy can be accounted for in three different ways: (1) The mammalian fossil

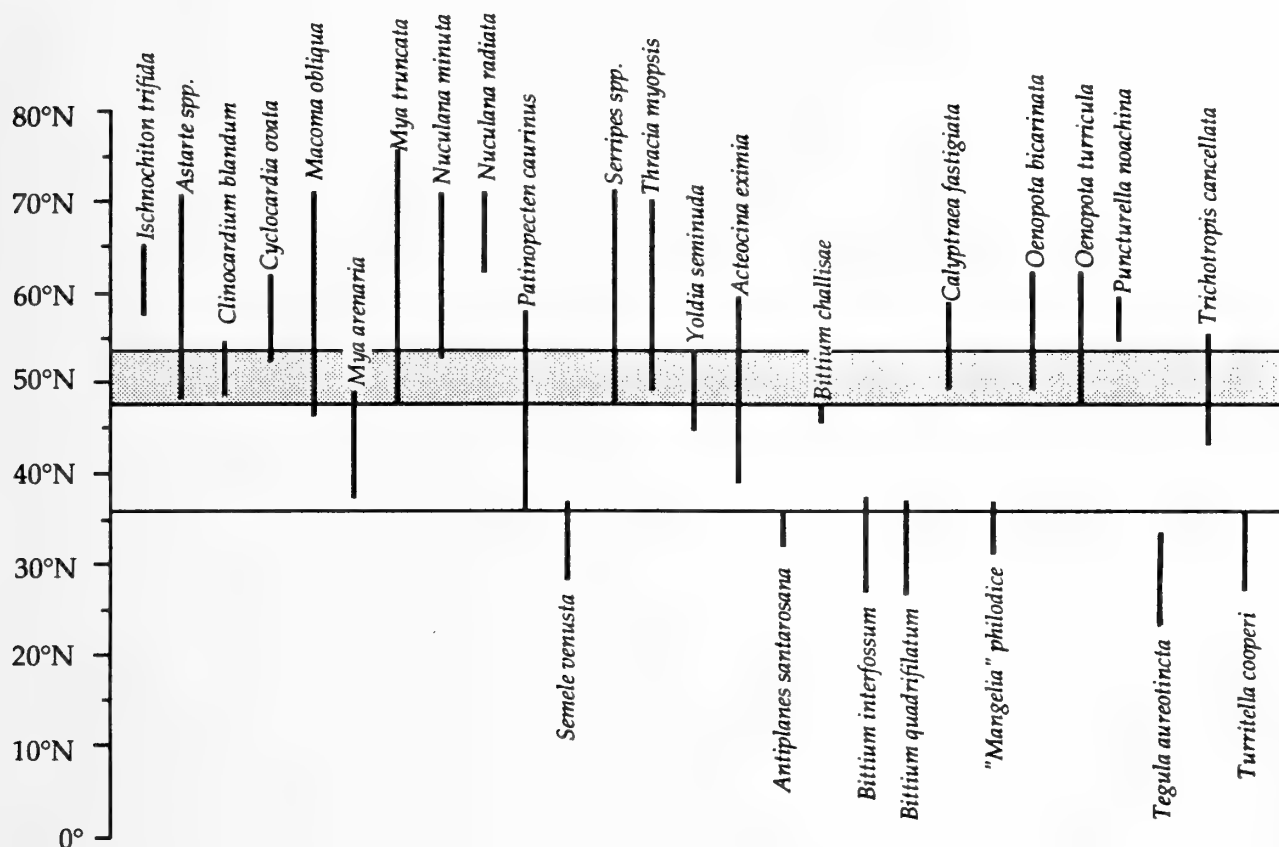


Figure 2

Latitudinal distribution of selected mollusks recovered from the Monterey Bay sea level lowstand deposits. The gray range bar shows the zone of maximum overlap of mollusk distributions at 48°N to 54°N, or from 12° to 18° north of the latitude from which the fossils were collected, which is marked by a line. The names of northern extralimital mollusks are printed above the range bar. Those whose distribution ranges south from the latitude of the fossil locality and are considered probable modern contaminants are named below the range bar.

record is represented by unusual individuals that traveled well south of their normal range. This interpretation seems unlikely, as three specimens have been collected. Recovery of a single specimen could be written off as a fortuitous individual, but the occurrence of three individuals that represent two separate taxa suggests the presence of a larger population due to much colder water conditions; (2) Both the mollusks and foraminifers contain significant modern contamination, thus yielding warmer paleoenvironmental interpretations; or (3) The fossil mammals are of a different age than the mollusks. This interpretation seems unlikely because ^{14}C age determinations for both the mollusks and Steller's Sea Cow are in general agreement (17,000 yr B. P. for the mollusks, and 19,000 yr B. P. for the Steller's Sea Cow; both fall within the sea level lowstand from 20,000 to 15,000 yr B. P.). I favor the second interpretation because the molluscan fauna examined here contains recognizable modern or submodern contaminants.

Annual sea-surface temperatures near the Aleutian Islands generally average about 5°C (Robinson, 1957). In

contrast, the region around Puget Sound and southern British Columbia records annual temperatures around 10°C to 11°C (Robinson, 1957), while annual sea-surface temperatures in the vicinity of Monterey Bay are about 13°C (Robinson, 1957). Based on the above marine mammal fossils, water temperature during the sea level lowstand was about 8° cooler than at present, whereas the marine mollusks suggest temperatures only 2° and 3° cooler.

SUMMARY

Fossil mollusks recovered from a sea level lowstand deposit in Monterey Bay, central California suggest that much cooler water conditions existed in Monterey Bay about 17,000 year B.P., with conditions essentially equivalent to present-day temperatures from Puget Sound, Washington to southern British Columbia (2° to 3° cooler). Marine mammal fossils from the same area suggest even colder temperatures, similar to those of the latitude of the Aleutian Islands (up to 10° cooler). The mollusks also suggest

much shallower water conditions (c. 10 to 50 m) than the 100 m to 300 m depth at which they were collected. *Chlamys rubida* collected from these deposits have given a ^{14}C age determination of about 17,000 yr B. P., which is generally equivalent to a worldwide sea level lowstand between 20,000 and 15,000 yr B. P., which was at least 100 m below modern sea level. Taking this lower sea level into view, the cooler and shallow-water aspect of the molluscan fauna from Monterey Bay is in full accord with the late Pleistocene paleogeography of Monterey Bay. The cooler and shallower water conditions are further supported by fossil foraminifers and marine mammals also collected from the vicinity of Monterey Bay.

ACKNOWLEDGMENTS

I thank John Chin for first drawing my attention to these fossils and Helen DuShane, Antonio Ferreira, Ronald Shimmek, and Thomas Yancy for loan of specimens and help in identification. I also thank George Kennedy, Dave Lindberg, Louie Marincovich, Mary McGann, Daniel Ponti, and William Sliter for helpful review of the manuscript. This manuscript was greatly improved by information acquired from a bivalve mollusk workshop held as part of the Western Society of Malacologists annual meeting and from Paul Scott, who has my appreciation.

APPENDIX: LOCALITY DATA

USGS M4492 (Field No.: MB10): Dredge haul from Monterey Submarine Canyon about 10 km offshore from Moss Landing (depth 120 to 275 m). Dredge started at latitude 36°45.54'N and longitude 121°56.60'W, and ended at latitude 36°56.55'N and longitude 121°56.55'W. Collected by Gary Greene, 1971.

USGS M5023 (Field No.: CB12): Dredge haul taken near the head of an unnamed tributary to Monterey Submarine Canyon about 10 km south-southwest of Point Lobos at a depth between 180 m and 300 m. Dredge started at latitude 36°25.90'N and longitude 122°00.00'W, and ended at latitude 36°27.10'N and longitude 121°59.00'W. Collected by Gary Greene, 1971.

USGS M9768 (Field No.: J283-3): Surface grab sample taken near latitude 36°45.45'N, longitude 121°55.18'W; at a depth of about 110 m. Collected by John Chin, 1983.

USGS M9769 (Field No.: J283-4): Surface grab sample

taken near latitude 36°45.44'N, longitude 121°55.12'W; at a depth of about 110 m. Collected by John Chin, 1983.

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International Workshop on the Marine Bivalvia of California

Food Choice, Detection, Time Spent Feeding, and
Consumption by Two Species of Subtidal Nassariidae
from Monterey Bay, California

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Abstract. Choice of food, time spent feeding, consumption and distance from which food could be detected were investigated for subtidal *Nassarius mendicus* and *N. perpinguis* (Neogastropoda; Nassariidae). Both species preferred fish but also fed upon bivalve carrion. We observed 110 and 25 feeding events on fish and bivalve carrion, respectively, by *N. mendicus* but only five feeding events upon both food types by *N. perpinguis*. Due to the meager feeding records for the latter, additional observations on food choice and time spent feeding were restricted to *N. mendicus*. The time spent feeding was inversely related to the number of times an individual fed, but *N. mendicus* fed quickly, usually for less than ten minutes. Of those individuals which fed more than once, the mean interval between meals was 3.14 days.

Neither species was capable of effective distance chemoreception of food. The food searching behavior which characterizes distance chemoreception by intertidal nassariids was evident only when individuals were in the immediate proximity to food (within 10 cm for *N. mendicus* or 2.5 cm for *N. perpinguis*). In contrast, contact chemoreception of food was well developed and usually elicited immediate feeding.

These results support our hypothesis that the subtidal habitat is not amenable to effective distance chemoreception typical of intertidal nassariids. Subtidal nassariids were found to be normally quiescent, buried in the substratum like their intertidal relatives. Unlike them, however, they probably respond only to carrion which falls nearby. They are apparently microphagous scavengers feeding upon small pieces of food that either slowly waft past or fall on or close to them. In view of the paucity of feeding records for *N. perpinguis* obtained during this study, the preferred food of this species remains to be determined.

INTRODUCTION

In a review of scavenging behavior by marine invertebrates, Britton & Morton (1993) concluded that there are no obligate marine carrion feeders. We believe that, because of the ephemeral nature of carrion in the marine environ-

ment, such food cannot exert sufficient selective pressure to establish obligate scavenging as a mode of life. Most scavengers are, therefore, facultative, pursuing carrion-feeding behavior as a dietary supplement to another, typically predatory, lifestyle.

A few marine gastropods have been regularly regarded

as scavengers, including representatives of the Buccinidae, Melongenidae and Nassariidae. Representatives of the former two families, i.e., *Buccinum* (Dakin, 1912; Gros & Santarelli, 1986; Himmelman, 1988) and *Hemifusus* (Morton, 1985, 1986a, b, 1987) will consume carrion, but are normally bivalve predators (Nielsen, 1975; Morton, 1985, 1986b). Only representatives of the Nassariidae come close to the definition of obligate scavengers (Britton & Morton, 1993), although this species-rich family has representatives which feed on a variety of food items. *Bullia digitalis* and *Nassarius krassianus*, both from South Africa, and *Ilyanassa obsoleta* from North America, for example, can survive on algae (Scheltema, 1964; Curtis & Hurd, 1979; Brown, 1982; da Silva & Brown, 1984; Harris et al., 1986), although *B. digitalis* is also known to consume live prey (Brown, 1971; Brown et al., 1989) and all consume carrion when it is available. *Nassarius trivittatus* from the temperate western Atlantic feeds on gastropod egg capsules (Kilburn & Rippey, 1982). Two intertidal species, *Nassarius pyrrhus* from Western Australia and *N. festivus* from Hong Kong, have only been observed feeding on carrion in the field (Morton & Britton, 1991; Britton & Morton, 1992), and the rate at which these species detect and move toward it, i.e., a mean arrival time of ~ 9 minutes for *N. festivus* (Britton & Morton, 1992), suggests that this is their major source of food.

Britton & Morton (1993) argue that nassariid scavenging behavior is strongly favored on gently sloping sand beaches experiencing moderate wave action, a moderate to large tidal amplitude and slowly receding tides. Water flowing over carrion picks up chemical cues from the moribund tissue and carries them considerable distances. Nassariids detect the cues by chemoreceptors, follow them speedily to their source, and eventually consume the stranded carrion. Large aggregations of nassariid scavengers often occupy beaches with these characteristics, and intertidal nassariids have been the focus of most research on gastropod scavenging (e.g., Atema & Burd, 1975; Crisp, 1978; Curtis & Hurd, 1979; Brown, 1982; Edwards & Welch, 1982; Race, 1982; McKillup & Butler, 1983; Stenton-Dozey & Brown, 1988; Brown et al., 1989; Morton, 1990; Morton & Britton, 1991; Britton & Morton, 1992).

Little is known about the feeding preferences of subtidal gastropod scavengers, especially the Nassariidae. Several subtidal gastropods such as *Buccinum undatum* and *Babylonia lutosa* are attracted to carrion, but these large whelks are also predators attracted to specific prey. *B. undatum* normally consumes bivalves and polychaetes (Taylor, 1978); *B. lutosa* also feeds on polychaetes and crustaceans (Morton, 1990). A recent monograph of the Nassariidae (Cernohorsky, 1984) clearly demonstrates the paucity of information on the food preferences of the majority of species, especially subtidal ones.

Several species of subtidal Nassariidae occur off the coast of California (Morris, 1966). We obtained two of these, *Nassarius mendicus* (Gould, 1849) and *N. perpinguis* (Hinds, 1844), during July 1991 from Monterey Bay. Hodgson & Nybakken (1973) found *N. mendicus* abundant (den-

sities up to $16.33 \cdot \text{m}^{-2}$) in Monterey Bay at a depth of 16 m in sandy mud sediments (65% sand, 35% silt/clay). They also found it at depths ranging from 14.5 to 63 m in sediments with variable sand:silt/clay ratios (sand fractions ranging from 14.9 to 94.5%). *N. perpinguis* was less common, with densities never exceeding $0.1 \cdot \text{m}^{-2}$. It occurred in sediments with high sand fractions (78.4 to 96.9%) ranging in depth from 15 to 36 m. The diets of these species are unknown; they may be predators, but they also scavenge, as we will show. Having completed several studies on intertidal nassariid scavengers (Morton, 1990; Morton & Britton, 1991; Britton & Morton, 1992) and having hypothesized about the possible habits of subtidal scavengers (Britton & Morton, 1993), we wanted to initiate work on the poorly known subtidal nassariids. We have postulated, for example, that the subtidal habitat, in the absence of strongly directional currents as occur during receding tides on sandy beaches, would not be amenable to effective distance-chemoreception typical of intertidal nassariids (Britton & Morton, 1993). Notwithstanding, carrion is available to the subtidal benthos, and subtidal nassariids probably exploit it like their intertidal counterparts by eating a lot quickly. We thus determined to test these two hypotheses using the subtidal nassariids, *N. mendicus* and *N. perpinguis*.

MATERIALS AND METHODS

Benthic samples were collected using a small biology trawl (Menzies, 1962) off Moss Landing, Monterey County, California on 6 and 11 July 1991. Most living specimens of *Nassarius mendicus* were obtained from samples collected at water depths of 30–32 m ($36^{\circ}48'70''\text{N}$, $121^{\circ}48'63''\text{W}$), whereas most specimens of *N. perpinguis* were obtained from samples collected at depths of 50–55 m ($36^{\circ}49'70''\text{N}$, $121^{\circ}50'25''\text{W}$). Most living individuals of both species were removed from the sediment while aboard ship; others were sorted from the sediment in the laboratory within six hours of collection. All *N. mendicus* collected on 6 July ($n = 133$) were placed in sand in a plastic tub measuring approximately $30 \times 23 \times 9$ cm. This was, in turn, submerged in an aquarium filled with 0.42 m^3 of micropore-filtered seawater maintained at a constant temperature of 10°C . Individuals of *N. perpinguis* collected on 6 July ($n = 35$) were held in a similar, separate plastic tub placed within the same constant temperature aquarium. These individuals were the subjects of the primary feeding experiments conducted in the aquarium.

Preliminary food preference experiments were conducted for both species by offering each a variety of living and dead food items, including polychaetes, small crustaceans, bivalves, and fish tissue. During these initial choice experiments, only fish and bivalve carrion were fed upon by both species. These food items were selected for more extensive food choice and feeding time studies.

Two food items, bivalve (*Mercenaria mercenaria*) ctenidia and red snapper (*Lutjanus* sp.) muscle, were placed in each of the nassariid containers for 1.5 hr daily for nine

consecutive days. Individuals were permitted to feed *ad libitum* during each feeding period. Feeding duration was considered to be the time between when the proboscis was first extended at the bait and when the scavenger subsequently abandoned it. After each feeding event, the shell length of each individual was measured and marked for subsequent identification. The food selected and feeding duration were also recorded.

Prior to and immediately following each feeding experiment, the wet weight of each food item was determined to the nearest 0.001 g, as were similar-sized controls which were not subjected to ingestion by nassariids. Wet and dry weights of fed-upon tissues and controls were determined. Wet weights of controls were used to determine weight changes, if any, of the food tissues when exposed in seawater during the feeding period. Dry weights of controls were used to estimate dry weights of tissues ingested. Consumption of each bait each day was considered to be the difference in food tissue weights before and after exposure to nassariid feeding, adjusted for weight loss or gain according to regression equations determined for the controls. Amounts ingested by each feeding individual were determined as a percentage of the total tissue ingested, prorated according to the individual and the time each spent feeding.

At the end of the feeding experiments, the nassariids were recovered, and wet weight, total dry weight, and dry tissue weight determined for each individual which fed. Consumption ($\text{mg dry food} \cdot \text{meal}^{-1}$) was related to nassariid size (shell length and dry tissue weight) and percentage of body weight ingested. Consumption rates ($\text{mg dry food} \cdot \text{day}^{-1}$) were determined for individuals which fed more than once.

Individuals collected on 11 July were held in separate containers, in the manner just described, and denied food except during experimental periods. Even then, they were removed from a food bait immediately upon being observed feeding on it. These individuals were used in experiments designed to determine each species' ability to detect food at various distances from it, in either the presence or absence of a strongly directional current. Fifty individuals of *Nassarius mendicus* and 50 individuals of *N. perpinguis* were used in the experiments. They were divided into subsets of 10 individuals, the shells of which were color-coded by fast drying epoxy paint of either red, blue, green, white, or yellow. Each color group was dispersed at varying distances from a bait, as described below. The distance from bait assigned to each color group was randomly selected each day.

The experimental design for food detection in the absence of a current employed a circular field covered with beach sand to a depth of about 1 cm. It was positioned in a shallow flow-through aquarium but experienced no directional water flow. Movements either within the aquarium or disturbances of the water surface by the investigators produced slight, ephemeral water movements in unpredictable directions. Bait consisted of $\sim 1 \text{ cm}^3$ of fish tissue which was placed in the center of the circular field and allowed to remain there for three hours each day or

until all experimental specimens were attracted to it, whichever occurred first. Each color group of experimental animals (10 *Nassarius mendicus* and *N. perpinguis* in each of the five color groups) were arrayed in concentric circles at distances of 2.5, 5, 7.5, 10, and 12.5 cm from the centrally located bait. Once arrayed, individuals were not disturbed if they either moved toward the bait or settled into the sand, but were returned to the original specified distance from the bait if they moved more than 5 cm outside the original release point.

The experimental design for food detection in the presence of a directional current employed an elongate tray along which flowed a broad stream of water at the mean rate of $0.43 \pm 0.05 \text{ cm} \cdot \text{sec}^{-1}$. The tray was filled with beach sand to a depth of about 1 cm. Bait, $\sim 1 \text{ cm}^3$ of fish tissue cut into an elongate strip, was placed at one end of the tray such that water flowed over it. The bait was allowed to remain in place for either three hours each day or until all specimens were attracted to it, whichever occurred first. Each color group of experimental animals (10 *Nassarius mendicus* and 10 *N. perpinguis* in each of the five color groups) were linearly arrayed at distances of 5, 10, 15, 20, and 25 cm downstream from the bait. Once arrayed, individuals were not disturbed if they moved toward the bait or settled into the sand, but were returned to the original specified distance from the bait if they moved more than 10 cm downstream from the original release point.

The time at which each individual commenced feeding on the bait was recorded in both flowing water and under static conditions, and the total numbers of each species reaching the food each day were tabulated. Individuals which began feeding were not permitted to complete a meal, but were removed from the experimental field, identified, and placed in a holding tank without food until the next day, when the experiment was repeated. Individuals were considered to be within detection distance of the food if (1) 50% or more from a specified distance reached the food and commenced feeding during the experimental period and (2) all groups positioned closer to the food were also found to be within detection distance.

Results of the five daily experiments for both species in flowing and non-flowing water conditions were respectively pooled to assess overall responses. The times to arrival at food by individuals of each species at each of the specified distances were compared by analysis of variance, and the cumulative frequency of specimens arriving and not arriving at food for each specified distance were compared by the Chi-square goodness of fit or contingency table analyses for both species in flowing and non-flowing water.

RESULTS

Food Choice and Time Spent Feeding

From 8–16 July 1991, we observed feeding by 91 individuals (68.4% of the experimental population) of *Nassarius mendicus* (Table 1) representing 110 feeding events upon fish tissue (81.5% of all meals) and 25 feeding events

Table 1
Summary of *Nassarius mendicus* feeding upon fish and bivalve carrion.

	Number of marked individuals feeding				Total individuals	Cumulative feeding events	Mean time spent feeding (min)	Mean SL (mm)
	Once	Twice	3 times	4 times				
First time fed	54	32	3	2	91	91	9.95	9.91
Second time fed	—	32	3	2	37	128	9.16	10.13
Third time fed	—	—	3	2	5	133	6.04	10.03
Fourth time fed	—	—	—	2	2	135	5.38	11.33
Grand means							9.51	10.00

(18.5%) upon bivalve tissue (Table 2). Feeding *N. mendicus* ranged in size from 6.6 to 12.9 mm shell length and 5.30 to 27.40 mg dry tissue weight. Additionally, we observed five individuals of *N. perpinguis* feeding, each at a different time. Due to the meager feeding records for *N. perpinguis*, no additional analyses were performed on these data.

Fifty-four individuals of *Nassarius mendicus* (59% of those which fed) fed only once during nine days of experiments, 32 individuals (35%) fed twice, three individuals (3%) fed three times, and two individuals (2%) fed four times (Table 1). Of the individuals which fed only once, 40 (74.1%) chose the fish and 14 (25.9%) chose the bivalve tissue. Of the individuals which fed twice, 21 (65.6%) had consecutive fish meals, 10 (31.2%) had one meal of fish and one of bivalve tissue (or *vice versa*), and only one (3.1%) had two consecutive meals of bivalve tissue. One individual which fed three times had three consecutive meals of fish, one interspersed a bivalve meal between two fish meals, and one had a final fish meal following two of bivalve tissue. Both individuals which fed four times ate only fish.

Table 2

Numbers of *Nassarius mendicus* which fed each day and the mean time spent feeding on fish or bivalve carrion.

Day	Total number feeding	Number feeding on fish	Mean time spent feeding on fish (min)	Number feeding on bivalve	Mean time spent feeding on bivalve (min)
1	40	29	7.41	11	12.57
2	20	17	10.65	3	18.76
3	9	6	6.41	3	5.06
4	43	39	11.18	4	11.65
5	1	0	—	1	14.00
6	6	6	5.95	0	—
7	7	4	4.00	3	9.48
8	1	1	5.88	0	—
9	8	8	6.42	0	—
Totals	135	110		25	
Means			8.93		11.95

The time spent feeding was inversely related to the number of times an individual fed. The mean time spent feeding by individuals which fed only once was 9.95 min, whereas it was 9.16 min for individuals which fed twice and 6.04 and 5.38 min for individuals feeding three and four times, respectively (Table 1). There was no apparent relationship between size (expressed as SL) and the number of times an individual fed (Table 1). The numbers of individuals which fed did, however, vary significantly from day to day. The greatest number of meals (43) occurred on the fourth day of the experiment, followed by 40 meals observed on the first day (Table 2). Twenty meals were taken on the second day, but less than 10 meals occurred subsequent to day four. Fish tissue comprised 81.5% of all meals; bivalve tissue, 18.5%. The duration of the average fish meal was 8.93 min; that of the average bivalve meal, 11.95 min (Table 2). The mean duration between meals for the 37 individuals which fed more than once was 3.14 days, with a range from one to eight days (Figure 1).

Consumption

The data just summarized, comprising all feeding events, were compiled during the course of the experiment. Subsequent analyses were performed on a reduced data set, due to escapes by some of the original experimental animals and a few apparently erroneous values associated with computed estimates (discussed below). At the end of the experimental period, we recovered 103 (77.4%) of the original 133 individuals placed in the holding tank. The unrecovered individuals, however, included some which had fed, reducing the number of fish meals available for subsequent analysis to 92 and the bivalve meals to 14, or a total of 109 feeding events. Consumption (mg dry weight of food·feed⁻¹) and percentage dry body weight ingested were calculated for each of these feeding events, and most produced apparently reasonable estimates. A few calculated consumption values exceeded three standard deviations of the mean and suggested that during one meal an individual ingested >100% of its dry body weight. These events were eliminated, and the analyses were repeated. Therefore, the final data set described below includes 66 individuals of *Nassarius mendicus* feeding 86 times on fish tissue and 13 times on bivalve tissue. *Nassarius mendicus*

ingested a mean of 1.69 ± 0.24 mg dry weight fish tissue \cdot feed $^{-1}$ ($n = 86$) and a mean of 0.452 ± 0.258 mg dry weight bivalve tissue \cdot feed $^{-1}$ ($n = 13$).

This study is not primarily concerned with scaling relationships, i.e., body size as a factor in the ecology of a species (LaBarbera, 1989), but some insights into the feeding behavior of *N. mendicus* can be inferred by comparing size and consumption variables. The most appropriate analysis of the relationship between two variables in which both are subject to large random error is a Type II regression (McArdle, 1988). We have conducted a more traditional analysis, however, in order to make direct comparisons between the subtidal species of this paper and previously published studies of intertidal nassariids.

The size of the feeding individual (expressed either as shell length or dry tissue weight) was a poor predictor of the amount of food ingested per meal for both fish (Figure 2A, B) and bivalve tissue (Figure 3A, B.). Although the slopes determined from least-squared regressions of log-transformed data indicated a slight positive relationship between these variables (Figures 2A, B; 3A, B), the coefficients of determination (r^2) were very low. Shell length, being a directly determined rather than a calculated variable, generally contained less measurement error variability than the calculated dry tissue weight determinations. This is clearly expressed by the coefficients of determination for the size-consumption relationships for *N. mendicus* feeding on fish (Figure 2A, B), but not apparent in the more limited data set for *N. mendicus* feeding on bivalve tissue (Figure 3A, B).

Daily consumption rates determined for individuals feeding on fish more than once also indicated a positive relationship between size (mg dry tissue weight) and food ingested, but again, the coefficient of determination indicated that size was a poor predictor of consumption (Figure 2D), at least with respect to the range of sizes available for study. The mean amount of food consumed by the 22 individuals which compose Figure 2D was 0.225 ± 0.008 mg dry weight fish tissue \cdot day $^{-1}$. There were insufficient numbers of *N. mendicus* feeding upon bivalve tissue more than once to make a similar determination.

When consumption was expressed as a percent of dry body weight consumed, the slope determined from a least-squared regression of log-transformed data indicated an inverse relationship between size and food ingested (Figure 2C), but the coefficient of determination for the allometric equation expressing this relationship was again very low.

The relationship between time spent feeding and consumption (expressed as mg dry wt of tissue consumed \cdot feed $^{-1}$) is enlightening when examined on a daily basis (Figure 4). As the amount of food consumed was assumed to be a function of time spent feeding, data points for each day produce a perfect linear correlation. More important, however, are the varying slopes of each daily regression, which reflect the relative amounts of food ingested by all feeding individuals that day. The moderate slopes for 9 and 11 July reflect reduced consumption (less food ingested

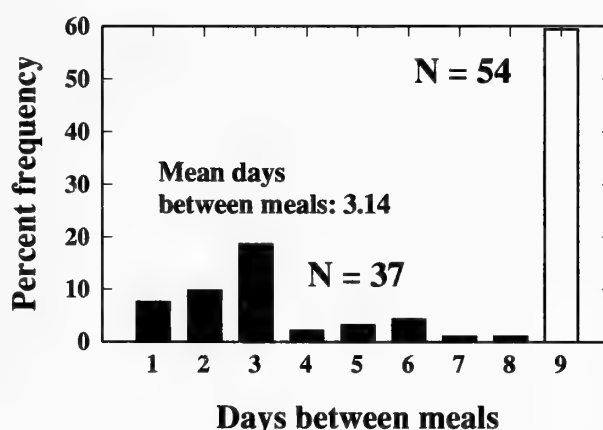


Figure 1

Percent frequency histogram of the number of days between meals. The solid bars represent individuals which fed more than once during the experiment, the unshaded bar those individuals which fed only once.

per unit time) and the steeper slopes of 8, 10, and 13 July reflect increased consumption (more food ingested per unit time). Regardless of how many individuals fed each day, therefore, consumption initially fluctuated from high to low and *vice versa* during the early days of the experiment, and concluded with high values for consumption at the end of the experiment; i.e., 14 and 16 July (Figure 4).

Food Detection

Results of the experiments designed to determine the ability of *Nassarius mendicus* and *N. perpinguis* to detect food at various distances in the presence or absence of a strongly directional current are summarized in Figures 5, 6, and 7 and Table 3. We recorded considerable daily variation during the course of the five days of experiments for both species in flowing and non-flowing (static) water (Figure 5). *Nassarius perpinguis* was never attracted to food in sufficient numbers for us to claim confidently that any of the tested distances (2.5 to 12.5 cm in static experiments; 5 to 25 cm in flowing water) were within the detection range of this species (Figures 5 and 7). Even when the five days of data were pooled, Chi-square goodness of fit analysis failed to detect any significant deviation from equality between the number of individuals arriving or not arriving at food from any of the tested distances. Similarly, we found no significant difference in the time of arrival of individuals from each of the specified distances for *N. perpinguis* in either flowing water (five-day pooled data, $n = 18$, $F = 0.211$, $\alpha = 0.05$, $P = 0.93$) or in the absence of flow (five-day pooled data, $n = 16$, $F = 1.21$, $\alpha = 0.05$, $P = 0.35$). One must conclude from these data that *N. perpinguis* is poorly equipped for remote detection of food from a distance of even 2.5 cm. Rather, it appeared that random encounters with a large food item induced it to stop and feed.

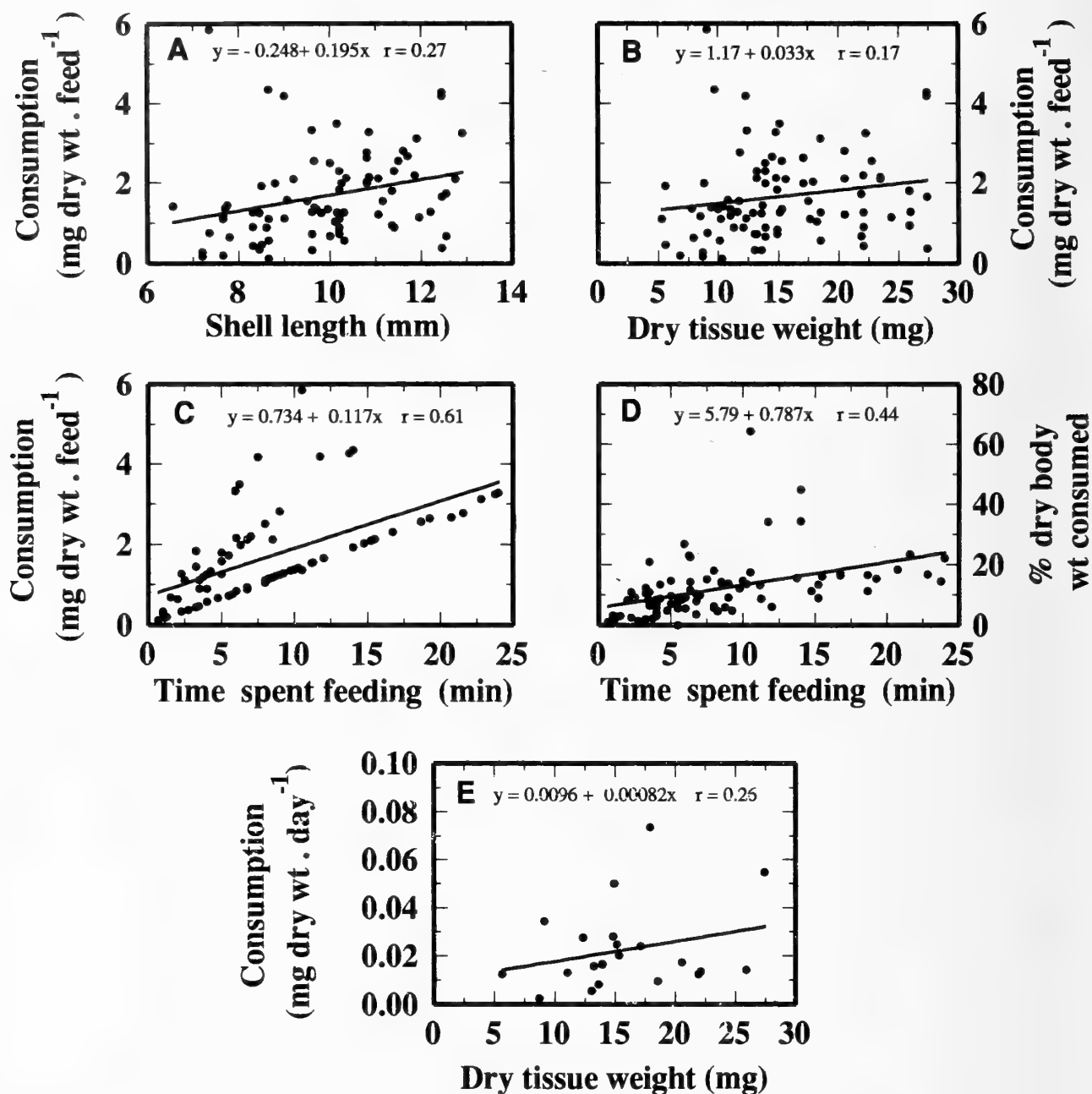


Figure 2

Nassarius mendicus feeding upon fish carrion. A. Consumption of food ingested in one meal vs. shell length. B. Consumption of food ingested in one meal vs. dry tissue weight of the feeding nassariid. C. Percent dry body weight consumed in a single meal vs. dry tissue weight of the feeding nassariid. D. Daily consumption rate vs. dry tissue weight for those individuals which fed more than once during the experimental period. The independent variables for regression equations (x) are shell length (A) or dry tissue weight (B,C, and D).

Greater numbers of *Nassarius mendicus* arrived at food from shorter than longer distances in both flowing and non-flowing water during the five days of experiments (Figures 5 and 6). This does not, by itself, indicate remote detection of food, for the result would also be expected by

random encounters. In fact, there was no significant difference in the time of arrival of individuals at food from each of the specified distances for *N. mendicus* in either flowing water (five-day pooled data, $n = 81$, $F = 1.086$, $\alpha = 0.05$, $P = 0.37$) or in the absence of flow (five-day

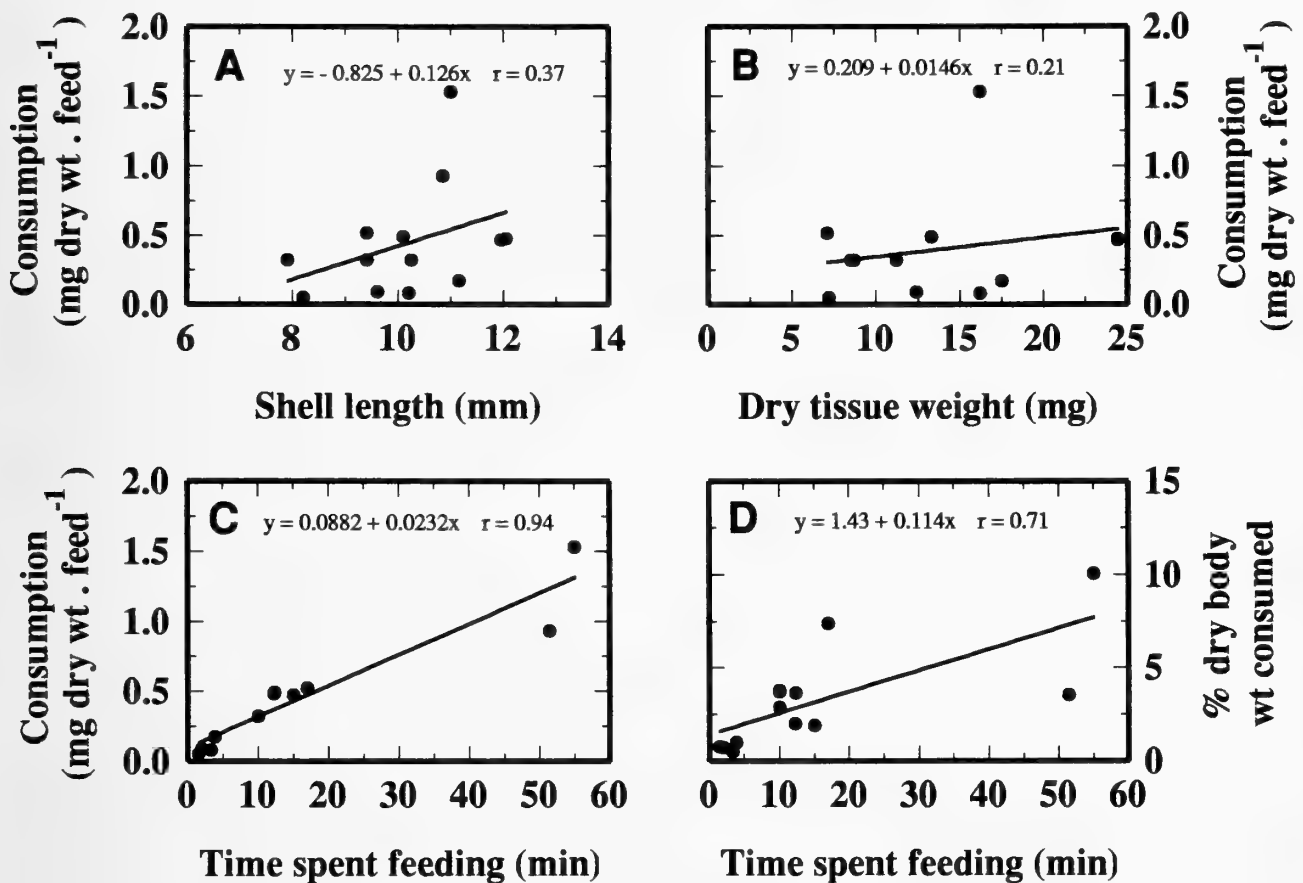


Figure 3

Nassarius mendicus feeding upon bivalve carrion. A. Consumption of food ingested in one meal vs. shell length. B. Consumption of food ingested in one meal vs. dry tissue weight of the feeding nassariid. C. Percent dry body weight consumed vs. dry tissue weight of the feeding nassariid. Independent variables as in Figure 2.

pooled data, $n = 80$, $F = 1.55$, $\alpha = 0.05$, $P = 0.20$). Using the 50% rule, *N. mendicus* detected food in flowing water from a distance of 5 cm for four of the five days tested, and from a distance 10 cm in two of the five days tested (Figure 5). It also detected food from a distance of 2.5 cm in non-flowing water for two of the five days tested (Figure 5). When the five days are pooled, however, the 50% rule failed to indicate that this species detected food at any distance in either flowing or non-flowing water. When cumulative frequency distributions were analyzed by Chi-square contingency tables, the numbers of *N. mendicus* arriving from the several distances differed significantly in flowing water, but not under static conditions (Table 3). Thus, *N. mendicus* is better equipped for remote detection of food than *N. perpinguis*, especially in flowing water, but the detection distance is small, probably less than 10 cm.

When the two species are compared, the percentages of *Nassarius mendicus* arriving at food consistently exceeded those for *N. perpinguis* at all tested distances in both flowing and non-flowing water (Table 3). The relative proportions of the two species reaching food was not signifi-

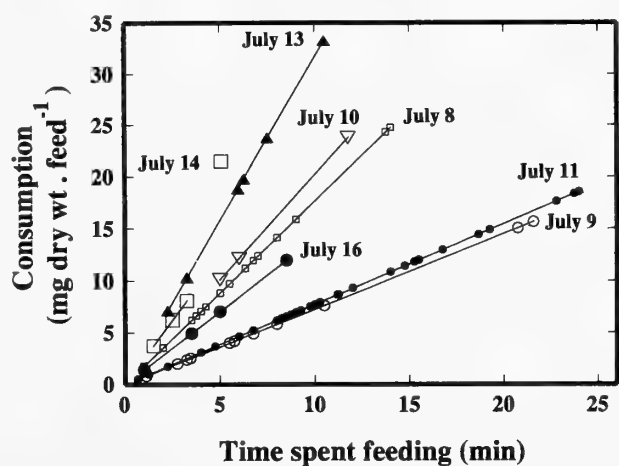


Figure 4

Nassarius mendicus. Consumption vs. time spent feeding on fish carrion. Note the pattern of changing slopes from day to day. The steeper slopes indicate more rapid feeding; the less inclined slopes represent slower feeding.

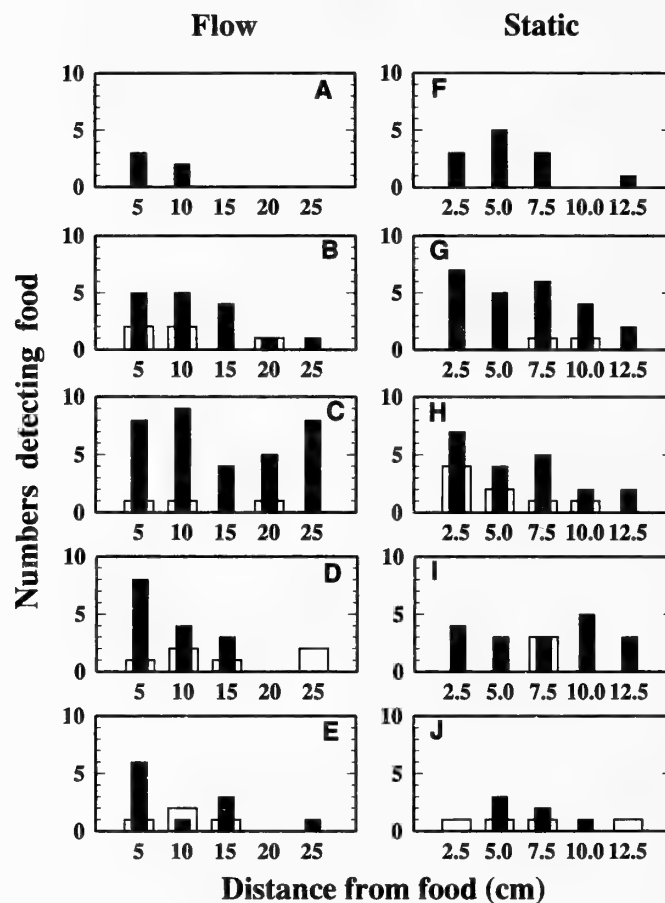


Figure 5

Numbers of *Nassarius mendicus* (narrow, solid bars) and *N. perpinguis* (wider, unshaded bars) attracted to food from various distances in flowing (A-E) and non-flowing (static) sea water. A. and F. First day of experiment. B. and G. Second day of experiment. C. and H. Third day of experiment. D. and I. Fourth day of experiment. E. and J. Last day of experiment.

Table 3

Cumulative (five days) frequency distributions of feeding nassariids arriving from specified distances in flowing and non-flowing (static) seawater. The frequency of arrivals for all distances was tested by contingency tables with critical Chi-square values determined for $\alpha = 0.05$. Significant deviation from equality by specimens positioned at different distances from food is indicated by an asterisk; the percent of the total number of individuals reaching food is given in parentheses.

Distance from food (cm):	Flow:	5.0	10.0	15.0	20.0	25.0	d.f.	Chi-square
	Static:	2.5	5.0	7.5	10.0	12.5		
<i>Nassarius mendicus</i> (flow)		30 (20.0)	21 (14.0)	14 (9.3)	6 (4.0)	10 (6.7)	4	25.0*
<i>Nassarius mendicus</i> (static)		21 (14.0)	20 (13.3)	19 (12.7)	12 (8.0)	8 (5.3)	4	9.1
<i>Nassarius perpinguis</i> (flow)		5 (3.3)	7 (4.7)	2 (1.3)	2 (1.3)	2 (1.3)	4	6.0
<i>Nassarius perpinguis</i> (static)		5 (3.3)	3 (2.0)	6 (4.0)	2 (1.3)	1 (0.7)	4	5.2

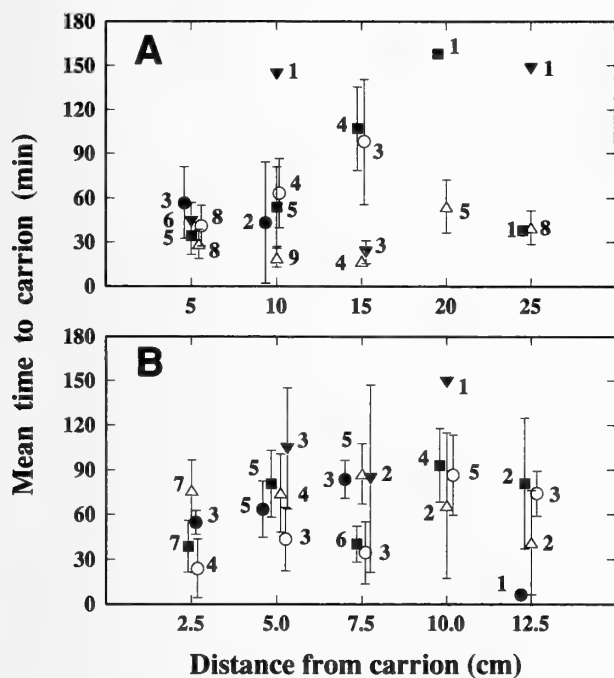


Figure 6

The mean time to arrival at fish carrion by *Nassarius mendicus* positioned at various distances from it in A, flowing and B, non-flowing (static) seawater. Numerals indicate the number of specimens represented by each data point. Bars indicate the standard error of the mean. Data points deviate slightly from assigned distances for clarity of presentation. The adjusted positions of data points in the figure do not reflect different spatial relationships during the experiment. Symbols are as follows: shaded circles, first day of the experiment; squares, second day; unshaded triangles, third day; unshaded circles, fourth day; shaded triangles, last day of the experiment.

cantly different in either flowing or non-flowing water, whether as comparisons between specific distances (i.e., 5 and 10 cm) from food ($\chi^2 = 0.50$, d.f. = 1 in flowing water; $\chi^2 = 0.011$, d.f. = 1 in non-flowing water) or relative distances (5–25 cm for *N. mendicus*, 2.5–12.5 cm for *N. perpinguis*) from food ($\chi^2 = 1.61$, d.f. = 4, in flowing water; $\chi^2 = 1.45$, d.f. = 4, in non-flowing water).

DISCUSSION

The general pattern of consumption by *N. mendicus* was distinctive. They were hungry upon arrival in the laboratory with almost one-third (30.1%) feeding on the first day (Table 2). On day four, almost one-third (32.3%) of the laboratory population fed again. Such a collective hunger would not be anticipated if *N. mendicus* was an obligate predator. Rather, the fact that they moved rapidly to carrion on the first day suggests they recognized it as food and were hungry. If they did not naturally feed on carrion,

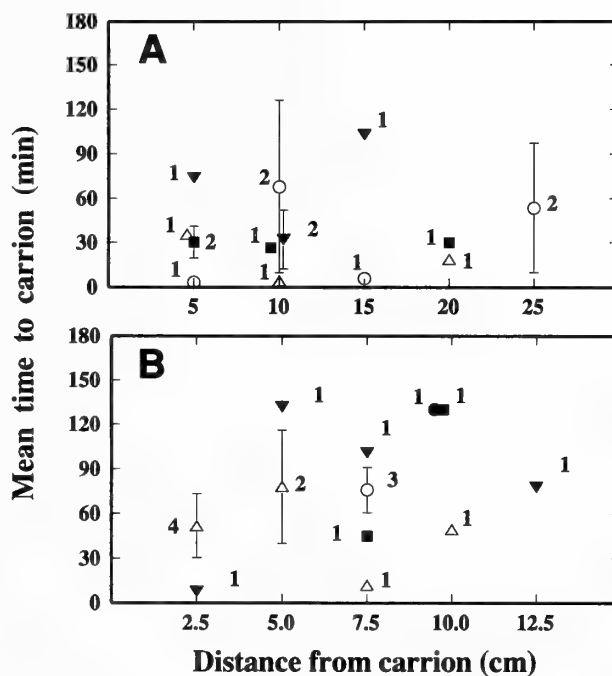


Figure 7

The mean time to arrival at fish carrion by *Nassarius perpinguis* positioned at various distances from it in A, flowing and B, non-flowing (static) seawater. Numerals indicate the number of specimens represented by each data point. Bars indicate the standard error of the mean. Arrangement of data points and meaning of symbols are as in Figure 6.

we could expect to see low feeding intensity on the first day, followed by increasing contact with and consumption of the bait as hunger set in, and the carrion progressively became more palatable. Most individuals which fed more than once during the experiment did so approximately every three days (Figure 1), giving, after the first day, another peak of feeding activity on the fourth day (Table 2). Thereafter, with hunger satiated for most of the individuals, they fed at a reduced frequency and for a progressively shorter period of time (Table 1). Such a picture is expressed most clearly in Figure 4 with peaks in consumption being recorded on 8 and 10 July, interspersed by low consumption on 9 and 11 July. Thereafter, on 13 July, consumption was again high, falling off on 14 and 16 July.

During both the feeding and food detection experiments, many *Nassarius mendicus* and *N. perpinguis* remained buried in the sand and were quiescent. Occasionally, individuals would emerge and crawl upon the surface. Only some

of these which came in close proximity to the carrion displayed the search pattern characteristic of their intertidal counterparts, the head moving from side to side with the siphon directed toward the food source and the proboscis everted in anticipation of feeding (Kohn, 1961). For those individuals which reached the food, feeding commenced almost immediately. Such a characteristic search pattern was displayed by many individuals coming near the food. Others, however, passed within a centimeter of the carrion without expressing recognition of it.

Intertidal nassariids often display acute distance chemoreception (Kohn, 1983). For example, *Nassarius festivus* in Hong Kong can detect carrion from ~2 m (Britton & Morton, 1992) and *N. pyrrhus* in Western Australia can detect it from ~1.5 m (Morton & Britton, 1991). In contrast, *N. perpinguis* failed to detect food as close as 2.5 cm, even in flowing water. *N. mendicus* performed somewhat better, detecting food from as far away as 10 cm. Successful feeding events by both species seemed to be as much the result of random encounters with food as the detection of it by distance chemoreception. *N. mendicus* and especially *N. perpinguis* responded to the presence of carrion only within their immediate vicinity. They displayed at least a limited capacity for distance chemoreception, because food searching behavior (eversion and searching motions by the proboscis) sometimes occurred prior to physical contact with the food, as observed in intertidal nassariids. They were thus not entirely limited to contact chemoreception in the sense described by Hodgson & Brown (1985) for *Bullia digitalis*, but their behavior during feeding and the results of food detection experiments indicated that contact chemoreception eclipsed distance chemoreception in these species. If an individual contacted food, even in the absence of distance food searching behavior, feeding usually ensued, suggesting an acute sense of contact chemoreception. These data thus corroborate our hypothesis (Britton & Morton, 1993) that deeper-water nassariids have a reduced capacity to move toward carrion, possibly the result of the reduction or absence of selection for distance chemoreception associated with physical attributes of the subtidal seabed, i.e., either a diminished or absent directional flow.

In terms of consumption, *Nassarius mendicus*, for which we obtained better data, acted similarly to its intertidal relatives after it commenced feeding. It fed to satiation quickly, consuming some 20% of its own body weight each feed. This corresponds closely with feeding rates observed for *N. pyrrhus* from Western Australia (Morton & Britton, 1991), *N. festivus* from Hong Kong (Britton & Morton, 1992), and *Bullia digitalis* from South Africa (Stenton-Dozey & Brown, 1988). *Nassarius mendicus* fed more frequently than *B. digitalis*, however, averaging 3.14 days between meals, whereas the latter fed every 7–10 days (Stenton-Dozey & Brown, 1988).

The strong scaling relationships between size and consumption documented by Stenton-Dozey & Brown (1988, Figure 1) for *Bullia digitalis* were less clear for *N. mendicus* (Figures 2 and 3), an apparent result of the respective

ranges of independent size variables. Using dry tissue weight to reflect size, *B. digitalis* individuals ranged from 16 to 1000 mg. In contrast, the dry tissue weights of *N. mendicus* ranged from 5.3 to 27.4 mg. Clearly, strong scaling relationships become more apparent as the range of sizes increases. It is not clear, however, if Stenton-Dozey & Brown (1988) would have discovered greater consumption variability for *B. digitalis* if they had examined as many individuals within restricted size range as was done for *N. mendicus*.

In summary, *Nassarius mendicus* recognized carrion, particularly fish. Newly captured individuals were hungry and fed rapidly for ~10 minutes. With progressive satiation, consumption and feeding time were reduced, as was the frequency between meals. Both *N. mendicus* and *N. perpinguis* were poorly equipped for distance chemoreception, even when a mechanism for long distance transport of chemical stimuli, i.e., a water current, was provided. This suggests that chemical stimuli carried by subtidal currents are of minimal importance to these species for food detection in their natural habitat and/or that these habitats are not normally subjected to directional currents. Both *N. mendicus* and *N. perpinguis* rely instead upon short distance and touch chemoreception to stimulate the characteristic nassariid feeding response.

These subtidal nassariids, therefore, are normally quiescent, buried in the substratum, like their intertidal relatives. Unlike them, however, they respond only to carrion which falls close to them. We must assume, therefore, that such animals are microphagous scavengers feeding upon small pieces of food that either waft past or fall on or close to them. They may also be predators, perhaps of polychaetes, but their initial unwillingness to feed upon living prey in the laboratory, the absence of any searching behavior typical of predators (Taylor, 1981), and their immediate recognition of carrion and feeding upon it, suggest that they are, like their intertidal relatives, at least facultative scavengers and perhaps have progressed a long way toward obligatory scavenging.

ACKNOWLEDGMENTS

We are indebted to Dr. James Nybakken and the staff of the Moss Landing Marine Laboratories, Moss Landing, California, for providing boat time to collect the specimens, and facilities to conduct the experiments. We are especially grateful to Paul H. Scott (Santa Barbara Museum of Natural History) who organized the bivalve workshop at Moss Landing, pointed us in the right direction when we needed various and sundry items to conduct the experiments, and graciously allowed us to pursue a decidedly non-bivalve project in an otherwise focused workshop. We are indebted to Maria Suarez at Texas Christian University who assisted with analysis of consumption by *N. mendicus*. David Cross, John Horner, and Gary Ferguson generously provided several measures of statistical expertise and advice.

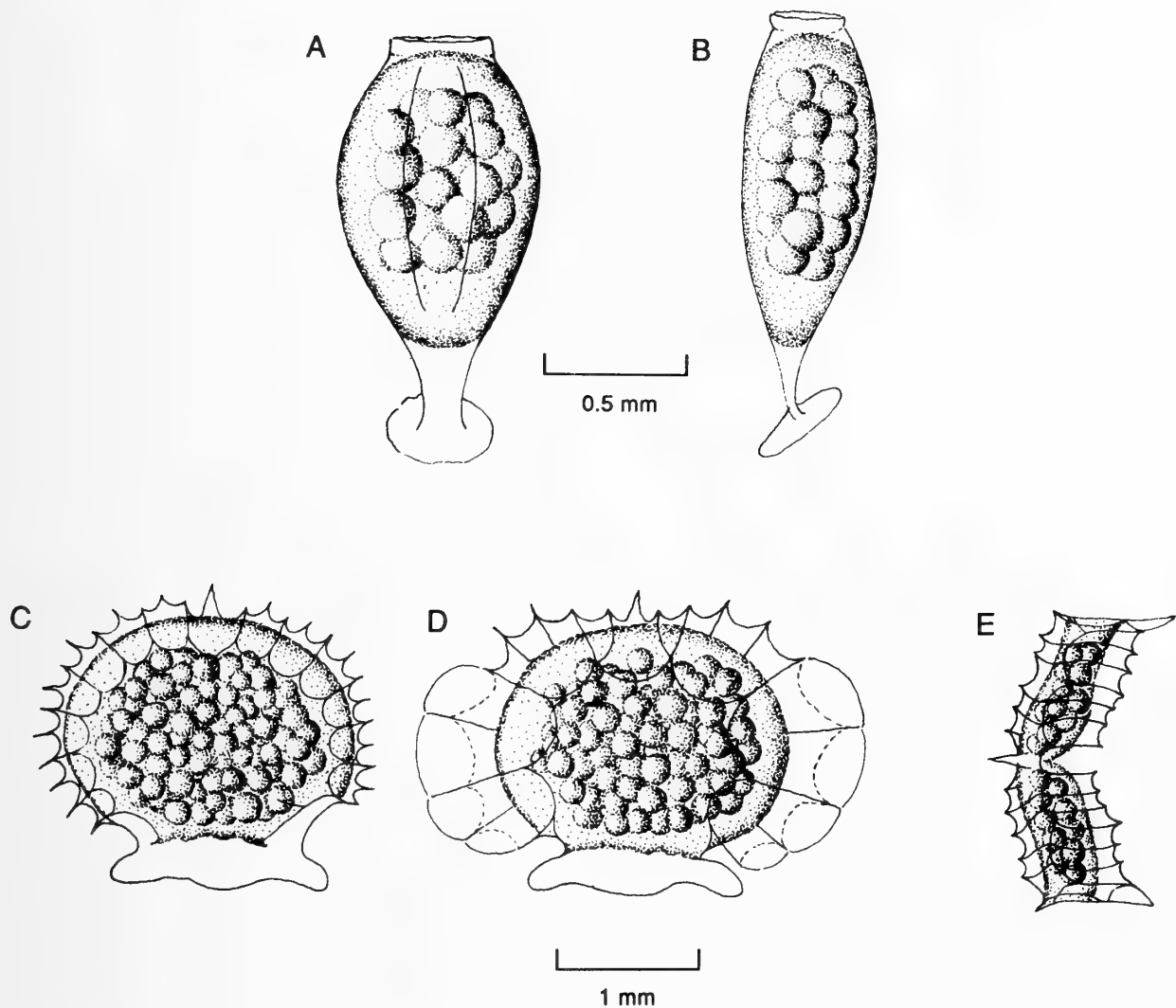


Figure 8

The egg capsules of A and B, *Nassarius mendicus* (front and side views) and C, D and E, *N. perpinguis* (anterior, posterior and dorsal views).

APPENDIX

During the course of our experiments, several individuals of *Nassarius mendicus* and *N. perpinguis* produced strings of egg capsules. That of *Nassarius mendicus* is flask shaped, attached at its base by a stalk, and layed in a long row. Each capsule was ~1.5 mm tall, 0.5 mm wide, and contained, on average, 20 eggs (Figure 8A, B). The egg capsule of *Nassarius perpinguis* is oval and also layed in rows. Each capsule overlaps the one in front and behind with a series of peripheral transparent projections, the largest of which are directed posteriolaterally. Each capsule was 2 mm tall, 2 mm wide, ~0.5 mm thick and contained large numbers of eggs (Figure 8C, D, E).

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Statocyst, Statolith, and Age Estimation of the Giant Squid, *Architeuthis kirki*

by

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Abstract. The statocyst and statolith of a mature female giant squid *Architeuthis kirki* Dell, 1970, caught in New Zealand waters are described. The organization of the chambers and internal projections of the statocyst can be interpreted as an analogue of a lamprey-like labyrinth with two semicircular canals. Size, sex, date of capture, and site of capture are reported for 24 *A. kirki* specimens caught in New Zealand waters from 1983 to 1988. A statolith from a specimen captured 3 May 1987 was sectioned and examined for microincrements, and the age assigned by assuming daily microincrementation. When size and date of capture are used to estimate annual growth rates, they yield rates similar to or slightly faster than those inferred from the statolith microincrements. Four different growth curves have been fitted to the length-at-age data: lowess (locally weighted least squares), exponential, logarithmic (power curve), and von Bertalanffy. Estimated von Bertalanffy curve parameters are $k = 0.0036d^{-1}$, and $L_{\infty} = 2168$ mm dorsal mantle length.

INTRODUCTION

The cephalopod statocyst has been considered functionally analogous to the inner ear of fishes (Stephens & Young, 1978). The overall shape and internal sculpturing of the statocyst of the cephalopod are thought to combine in such a way as to result in controlled flows of endolymph within the statocyst (Vinnikov et al., 1968; Budelman, 1977; Maddock & Young, 1984; Young 1984). In particular, the interlocking projections of the inner surface of the statocyst are thought to result in endolymph flow in different planes that mimics the vestibular labyrinth of fishes (Stephens & Young, 1978).

The statocyst of cephalopods also contains a statolith. Although there is a certain amount of variation in shape of statoliths among different cephalopods, there is a general similarity in shape, particularly among the squids (Clarke, 1978). The squid statolith has a similar internal structure to the teleost otolith, with a well-defined nucleus and concentric microincrements and check rings. Just as the stato-

cyst has been regarded as convergent on the teleost labyrinth, so has the statolith been regarded in structure, at least, as convergent on the teleost otolith. Statolith structures, particularly microincrements, have been used to age many species of squid following the assumption of daily deposition of microincrements (Hurley & Beck, 1979; Dawe et al., 1985; Lipinski, 1986; Jackson, 1990). In this paper we examine the structure of both the statocyst and statolith of a specimen of the giant squid, *Architeuthis kirki* Dell, 1970, that was recovered at sea in New Zealand waters in an excellent state of preservation.

In addition, we report size, sex, date and site of capture data from specimens of *Architeuthis kirki* caught in New Zealand waters between 1983 and 1988. These data can be used to infer growth curves. The growth of squid has been treated as implicitly convergent on teleost growth by virtue of the use of growth curve fitting procedures characteristic of teleosts, although several recent papers question the value of this assumption (e.g., Forsythe & Van Heukelem, 1987; Forsythe & Hanlon, 1989; Jackson &

Table 1

Architeuthis kirki reported from New Zealand waters, 1983–1988. All animals collected at sea unless otherwise noted.

Specimen number	Date	Dorsal mantle length (D.M.L.) mm	Sex	Location	Depth (m)
1	19 Aug 83	2035	U	39°03'S, 174°04'E	on shore
2	8 Mar 84	1930	F	51°16'S, 166°52'E	533
3	12 Apr 84	930	F	41°11'S, 176°44'E	870–1100
4	3 May 84	1770	F	40°54'S, 176°14'E	—
5	12 May 84	1825	F	41°17'S, 174°47'E	on shore
6	25 Jul 84	1560	F	41°05'S, 170°52'E	475
7	24 Sep 84	2020	F	46°18'S, 166°30'E	365
8	31 Mar 86	1720	F	50°50'S, 166°51'E	296
9	11 Apr 86	1260	M	35°43'S, 174°20'E	—
10	17 Apr 86	1815	F	43°38'S, 174°43'E	470
11	27 May 86	1830	F	46°32'S, 166°11'E	604
12	18 Jul 86	1380	U	42°03'S, 170°26'E	500
13	8 Sep 86	2140	F	43°43'S, 174°56'E	480
14	26 Feb 87	1900	M	44°09'S, 173°44'E	350
15	3 Apr 87	1610	F	41°31'S, 176°43'E	360
16	9 May 87	2135	F	43°38'S, 174°14'E	506
17	26 Jul 87	1300	U	42°35'S, 170°23'E	—
18	16 Aug 87	1370	U	41°21'S, 170°30'E	—
19	25 Aug 87	1230	F	41°31'S, 170°34'E	—
20	2 Sep 87	1780	U	51°18'S, 170°23'E	—
21	13 Oct 87	1770	U	46°24'S, 166°23'E	487
22	4 Nov 87	2010	U	47°32'S, 169°10'E	—
23	5 Nov 87	1770	U	46°31'S, 166°30'E	550
24	25 Jan 88	1880	U	51°00'S, 166°42'E	—

Choat, 1992). Analysis of date of capture and size at capture allows us to comment on the significance of the shapes of different growth curves for *A. kirki*.

MATERIALS AND METHODS

A total of 24 specimens of *Architeuthis kirki* were recovered between 1983 and 1988 in New Zealand waters. Size, sex (where known), site of capture, and date of capture are listed in Table 1. Site of capture is shown in Figure 1. Additional zoological data will be published separately (Förch, in preparation). Size is given as dorsal mantle length (DML) following Roper & Voss (1983), which is equivalent to "mantle length, along dorsal midline" proposed by Boyle (1986) and reported for *A. kirki* from South African waters by Roeleveld & Lipinski (1991).

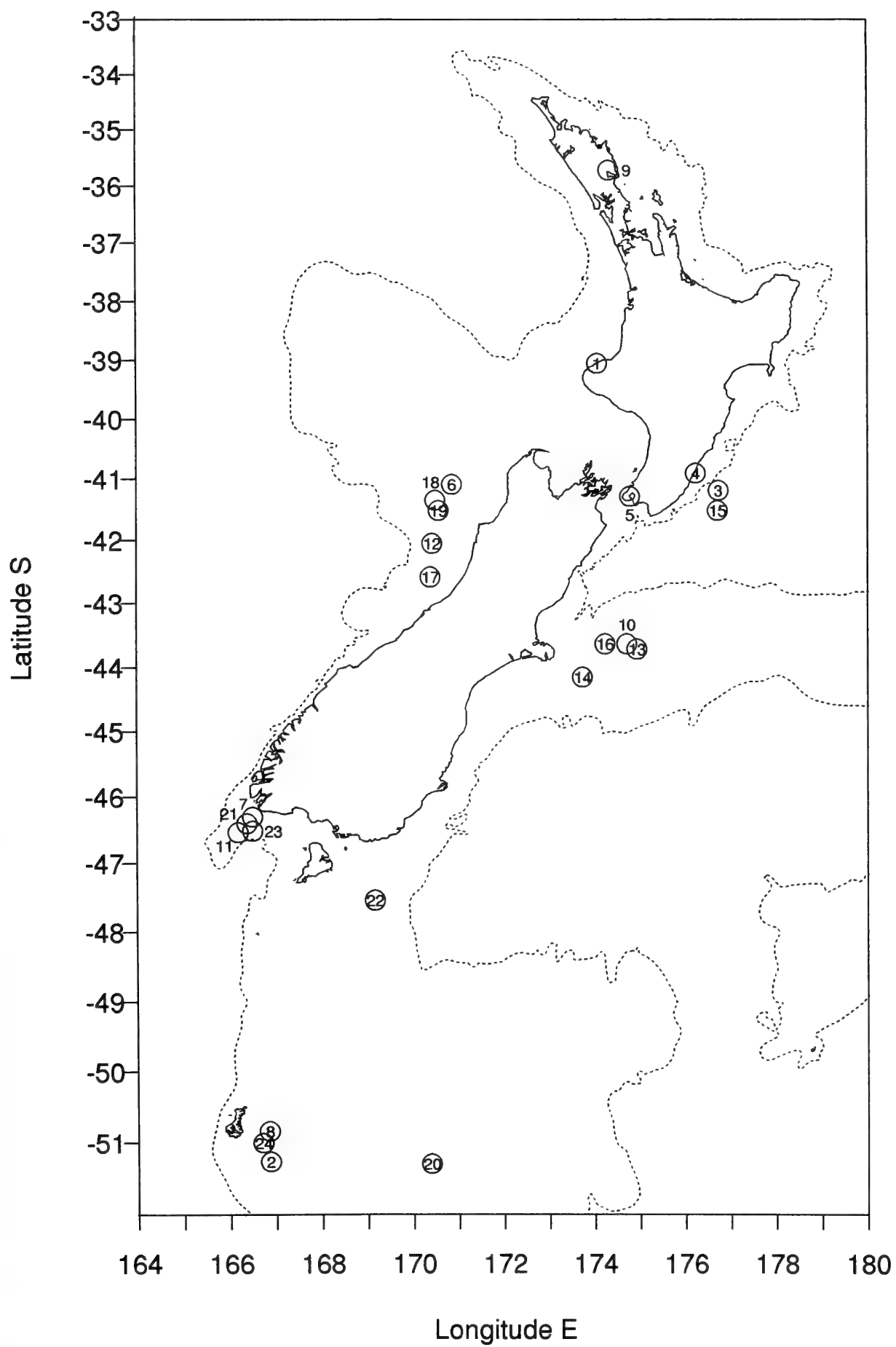
On 3 May 1987, a 1610 mm (dorsal mantle length) immature female *Architeuthis kirki* was recovered dead from the net of a trawler and frozen almost immediately at -20°C . After thawing for two days, the specimen was dissected at the Fisheries Research Centre, Wellington,

New Zealand, and the zoological characters necessary to identify the species were measured and recorded (Förch, unpublished data). During dissection, the paired statocysts of the head cartilage were removed, the internal structures photographed with a stereomicroscope, and the statoliths removed. Statoliths were mounted on stainless steel pin-stubs and photographed using a Philips 505 Scanning Electron Microscope. One statolith was removed from the pin-stub and ground with wet-and-dry 4000 grit paper along the axis from the nucleus to the anterior edge. Crystal structure is described in the appropriate terms for molluscan aragonite (Carriker et al., 1980) and general crystallography, and the terminology for internal structures follows the usage for teleost otoliths.

Growth curves were fitted either by the method of locally weighted least squares by using the lowess technique of Cleveland (1979), or by using the non-linear routines of S-PLUS (Chambers & Hastie, 1992) that uses the Gauss-Newton algorithm. Exponential, logarithmic, and von Bertalanffy curves were all fitted using non-linear routines.

Figure 1

Site of capture or stranding of 24 specimens of *Architeuthis kirki* reported in New Zealand waters 1983–1988. The numbers on the figure are the specimen numbers of Table 1, specimens being ordered by date of capture or stranding. The dotted line is the 100 m depth contour. The projection is Mercator.



RESULTS

1. Statocysts

The statocysts of *Architeuthis kirki* were in the form of a pair of small, oblong-shaped sacs ($18.6 \times 12 \times 9.5$ mm) and were about 25 mm apart, located in the head cartilage of the squid canted outwards about 30° from vertical and oblique to the longitudinal axis of the animal, in a similar orientation as reported by Roeleveld & Lipinski (1991). When opened from the external side, the right statocyst showed a few large internal projections and a statolith lying at the bottom of the sac (Figure 2). The part of the statocyst that had been removed to show the interior of the statocyst (Figure 2) had three internal projections. The most convenient way of showing the internal three-dimensional structure of the complete sac is by using a model (Figure 3A, B, C) in which the projections of the removed section have been replaced by three balls. The statolith is shown slightly oversize lying where it was first observed in the dissected sac. There were 10 projections in the statocyst, and a ridge-like structure divided the sac into an anterior and posterior chamber (Figure 3). The left hand statocyst was irrigated with methylene blue stain to identify nervous tissue. Some differential staining occurred, but it was not possible to identify any obvious nerve structure morphology. Our observations did not show anticristae of the form described by Young (1960) as "a rigid plate of cartilage" and by Wells (1979, pp. 158–159) as "a thin flexible plate with a rough spiny surface." The clearly identifiable anticristae of *Octopus* sp. have been homologized into hook-like projections in the squid statocyst (Dilly, 1976; Stephens & Young, 1978). Consequently, the projections of the statocyst of *A. kirki* have been characterized as hamulae and anticristae by Roeleveld & Lipinski (1991). However, we could not see a well-defined morphology in the statocyst of *A. kirki* upon which to base this distinction, nor did Roeleveld & Lipinski (1991) offer any morphological criteria to support such a distinction.

It has been proposed by Stephens & Young (1978) that the statocyst acts as an analogue to the semicircular canals of the inner ear of fishes. Following their argument, it is evident that any kind of analogue of the fish inner ear would have to act as an interconnected series of canals and ampullae. The system of chambers and spaces evident in Figure 2 can be reconstructed into a set of "canals" joining three "ampullae," as well as the chamber of the statolith. The reconstruction was carried out by first deciding which of the three chambers of the statocyst would be assigned the status of "ampullae." After that decision, the widest interconnecting spaces were assigned the status of "canals" to develop the schemata for vestibular function as shown in Figure 3C. Although this approach is no less subjective than that of Stephens & Young (1978), it follows the basic hydrodynamic requirements of a labyrinth in the sense that it first identifies fluid receptacles and then the interconnecting canals. The sensitivity of the vertebrate labyrinth to changes in angular momentum is given by the



Figure 2

The right-hand statocyst has been opened from the external side with anterior (A) below, and dorsal (D) to the left. The statocyst has large internal projections (arrow), and the statolith can be seen (open arrow) lying in the ventral (V) part of the most anterior chamber of the statocyst. A ridge (R-R) divides the statocyst into two chambers. The bar is 1.75 mm.

Jones & Spells (1963) statistic r^2R/V , where r is the radius of the bore of the canal, R is the radius of the canal, and V the average volume of the ampullae. The relation r^2R/V is a dimensionless ratio so that equivalent measurements can be made from Figures 1 and 2. Based on these figures, the value of r^2R/V is about 0.2, being smaller or larger depending on how "canal" is defined.

Presenting the internal structure of the statocyst as an analogue of the vertebrate semicircular canals is only one model. Another alternative model arises when one considers the basic hydrodynamics of fluids. The vestibular mechanism acts in a similar way to fluids held in a moving cup; rotating the cup induces motion in the enclosed fluid, which then continues to move when the cup comes to rest. In the vertebrate semicircular canals, fluid motion is induced by

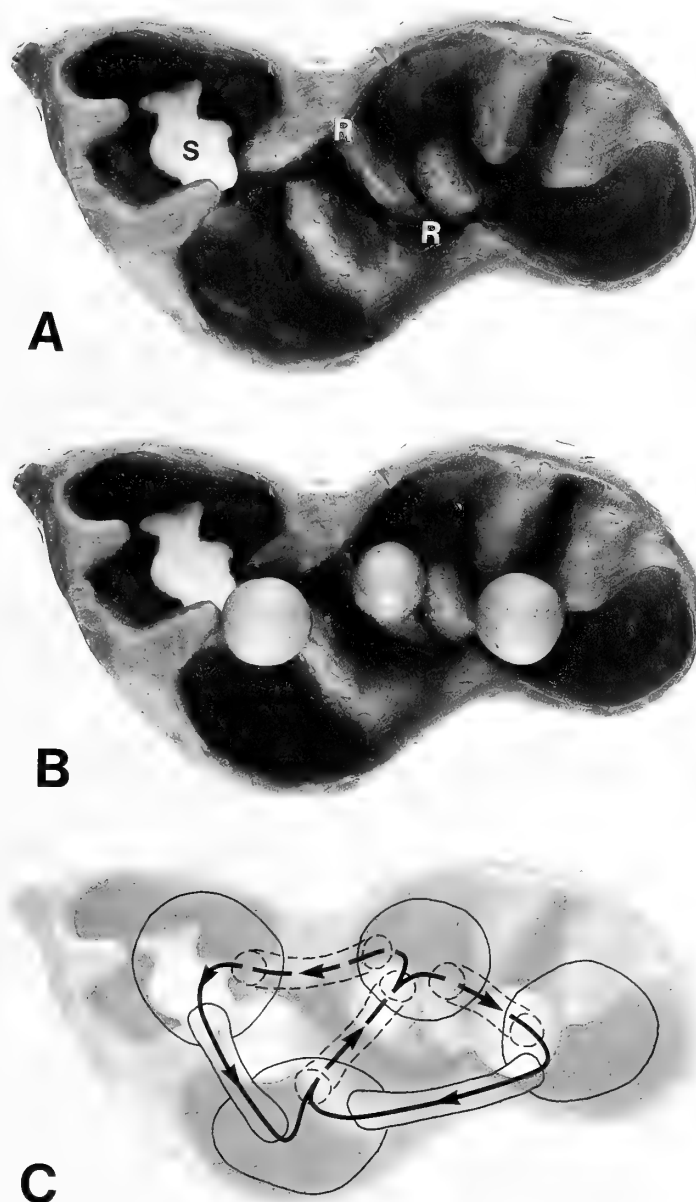


Figure 3

A. A plasticine model of the statocyst is shown with the dorsal to the RHS with the internal projections and the ridge (R-R) that divides the statocyst into a posterior chamber and an anterior chamber with a relatively larger than life size statolith (S). B. Three balls of plasticine are inserted as analogues of the projections that were on the lateral (viewer-facing) inner wall of the statocyst. C. Organization of the statocyst into possible "ampullae" (circles) and "canals" (arrowed lines) is shown as an overlay.

the movement of the head. Persistence of fluid motion is obviously undesirable, and the bore and ampullae system, particularly the progressive distortion of the cupola "gate" in the ampullae (Ten Kate, 1969), rapidly damps fluid motion. Thus the Jones & Spells (1963) statistic can be interpreted as both a measure of sensitivity to motion and as a measure of damping. Modeling the statocyst as an

analogue of the semicircular canals, both in our model and that of Stephens & Young (1978), plays down the "leakiness" that disables the damping requirements of such an analogue; yet it is evident from our model that the "leaks" are more obvious to the eye than the "canals" that our imagination projects on the statocyst. A much simpler model would be that of simple counter-rotating fluid flow that

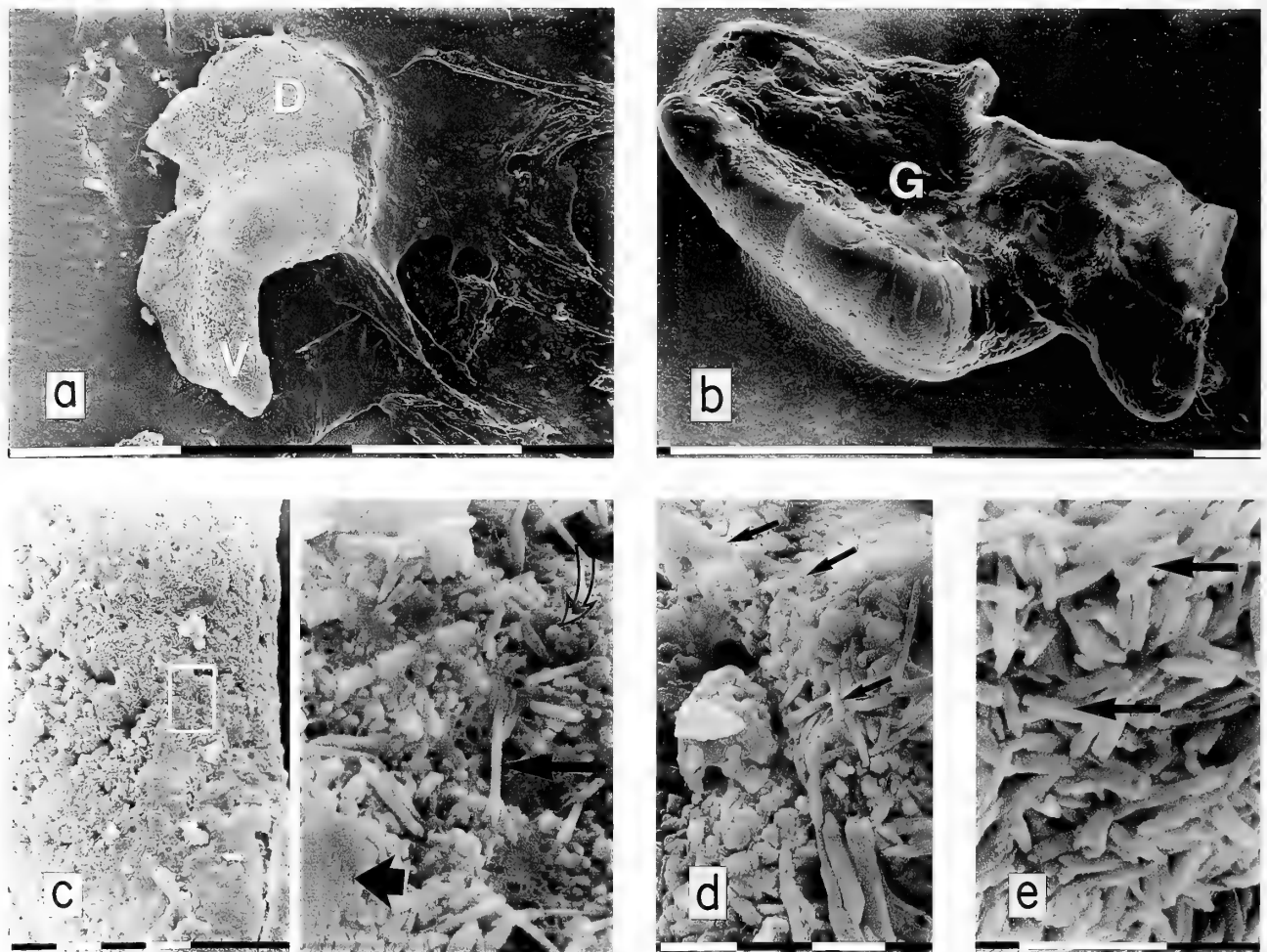


Figure 4

a. The external, anti-tissue-facing side of the statolith has a side dorsal (D) prism and a narrow ventral (V) prism separated by a dome-shaped structure that lies above the nucleus of the statolith. The bar is 1 mm. b. The internal, tissue-contact face of the statolith has a central groove (G) similar to the sulcus of some teleosts. The bar is 1 mm. c. Detail of the external surface (the RHS is an enlargement of the white box in the LHS) showed epitaxial crystals (open arrow) growing out of the body of the statolith and monoclinar aragonite crystals growing separately on the surface (arrow) and some indications of chalky concretions (long arrow). The bar is 50 μ m. d. Parts of the statolith surface show absorption (arrows) of the monoclinar aragonite crystals into the epitaxial crystals of the statolith. The bar is 50 μ m. e. Detail of the lower surface showed dense aggregations of aragonite crystals (arrows) on some parts of the surface. The bar is 50 μ m.

moves simultaneously from chamber to chamber. The effect of the internal projections of the statocyst would then serve as much to damp the flow by disturbing fluid movement, as they serve to canalize fluid movements in certain directions.

2. Statoliths

The right hand statolith of *Architeuthis kirki* is shown in Figure 4a from the posterior convex face. The anterior and ventral parts of the statolith are indicated in Figure 4a as the statolith was observed *in situ*. The lower, tissue-

contact face has a central groove analogous to the sulcus of some teleost otoliths (Figure 4b). Detail of the upper surface (Figure 4c) showed epitaxial crystals growing from within the statolith, covered with a scattering of single monoclinar aragonite crystals, in addition to chalky areas on the statolith surface (Figure 3c). Some parts of the upper surface showed evidence of absorption of the monoclinar aragonite crystals into the structure of the statolith (Figure 4a). In some parts of the statolith, the surface is completely covered with monoclinar aragonite crystals (Figure 4e).

A vertical section of the statolith along the anterior axis showed a continuous series of microincrements from the

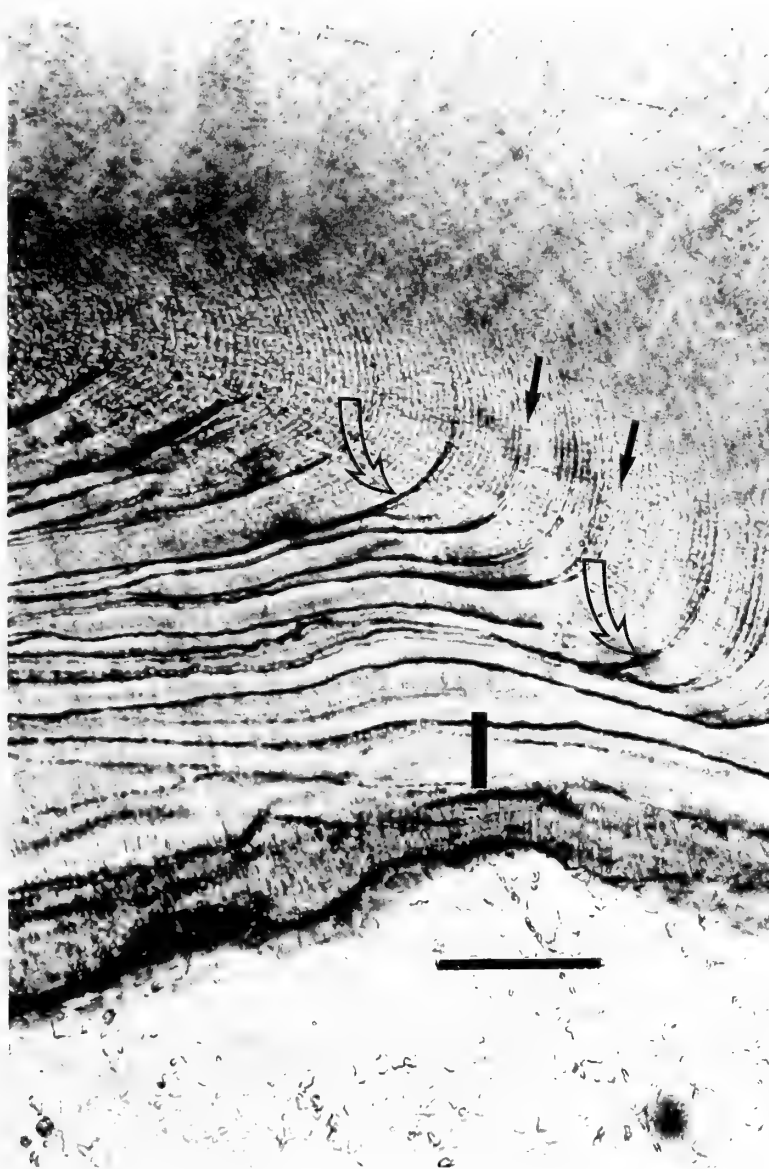


Figure 5

A vertical section of the statolith through the nucleus to anterior edge axis showed an orderly series of microincrements (arrows) and evidence of fusion of microincrements into check ring-like structures (open arrows) that characterize the tissue-facing internal (I) side of the statolith. The bar is 50 μm .

well-defined nucleus to the margin of the statolith, as well as fusion of the microincrements into more prominent check-ring type of structures in the anterior rostral region of the statolith (Figure 5). Counting micronutrients from the center of the nucleus of the statolith to the margin yielded 393 microincrements varying in width from about 2.5 μm near the nucleus to about 1 μm at the anterior edge of the statolith. Microincrements were clearly visible, and repeated counts yielded effectively the same number of microincrements: 391–395 in four trials.

3. Growth rate estimation

Data: The opportunity to examine the statolith of *Architeuthis kirkii* in sufficient detail to count microincrements came late in the collection program and was restricted to one medium size (1610 mm DML) specimen. However, the validity of the age implied by the assumptions of daily microincrements can be assessed from a consideration of size-at-time-of-capture for all of the giant squid recovered for this study.

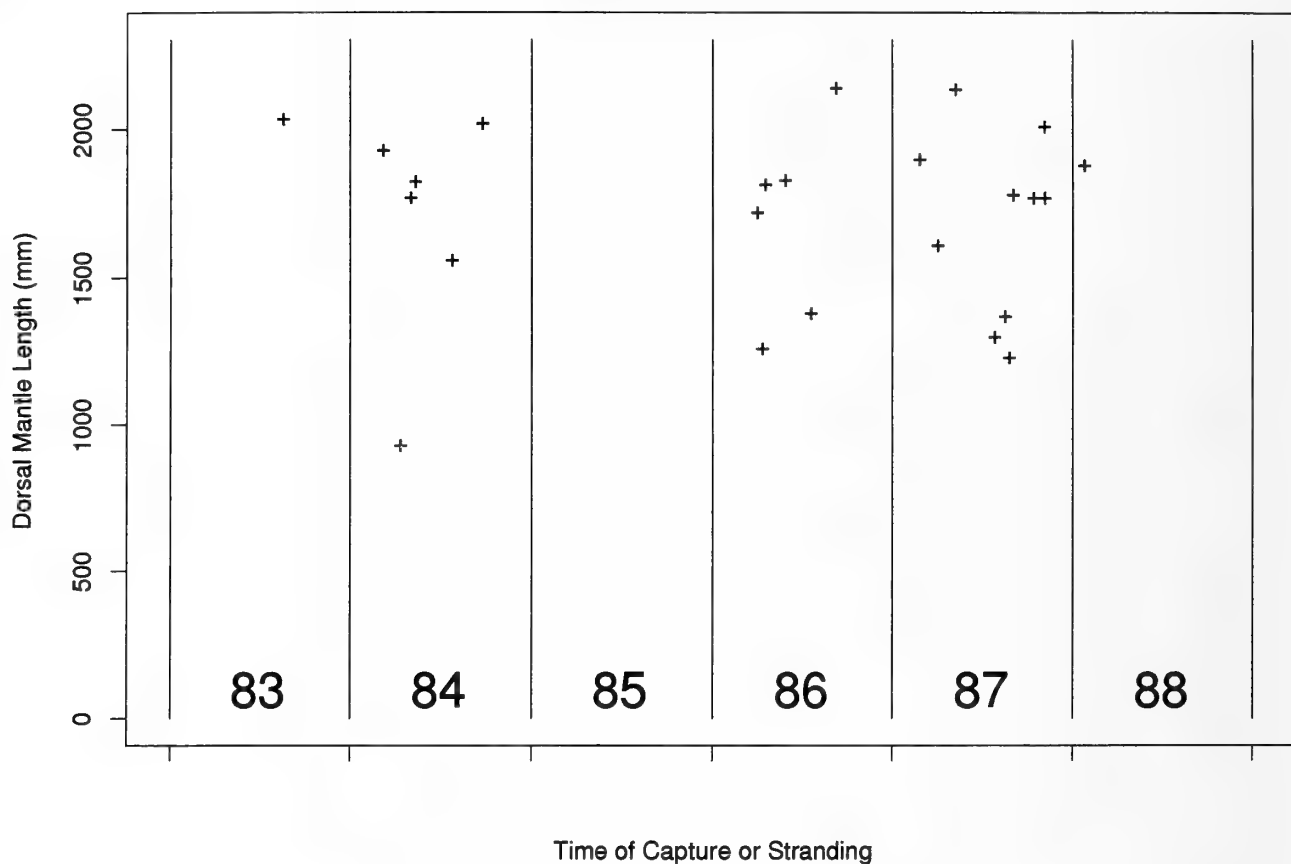


Figure 6

Date of capture plotted against dorsal mantle length (DML) for 24 specimens of *Architeuthis kirki* reported in New Zealand waters 1983–1988.

Date of reported capture or stranding is plotted against DML in Figure 6. We have no explanation for the gap in reportings in the 18 months between September 1984 and March 1986. Figure 7 shows DML plotted against the day of the year on which a squid capture or stranding was reported. The numbers shown on this figure are the specimen numbers of Table 1 and are in the order of date of reporting. No squid greater than 1560 mm DML were reported in any year in the 87 days between 27 May and 19 August. Four of the seven smaller squid were reported in this period, and another at six days after the end of the end of the period.

Translation of data: Life spans of large temperate-water squid are generally believed to be annual (Voss, 1983; Amaratunga, 1987; Natsukari et al., 1988; Rodhouse & Hatfield, 1990a, b). If this were also true for *Architeuthis kirki*, then Figure 7 could be generated by one or more of the following processes:

- (a) growth rates differing widely between years;
- (b) growth rates differing widely between individuals giving rise to Lee's phenomenon (Ricker, 1975) in which

larger, faster growing squid mature, spawn, and die in advance of slower growing members of the cohort (e.g., Rodhouse et al., 1988);

- (c) a year-round breeding season.

The gap in the capture of larger squid, noted above, suggests another possibility: animals above and to the left of the dotted line ABC in Figure 7 could be survivors from an earlier calendar year. We explored this possibility by plotting day-of-reporting against DML, with these animals translated to the next calendar year. Figure 8 shows animals above and to the left of the line ABC translated to the next calendar year. Figure 9 shows animals above the line ABD translated to the next calendar year.

Lowess and von Bertalanffy curves: We fitted a locally weighted least squares line to the data using the lowess technique of Cleveland (1979) to the data in Figure 8 and Figure 9. The locally weighted line was linear (degree = 1) and the locally weighted window (span) was $\frac{2}{3}$. The weighting function was the tricube function. This is essentially a non-parametric method, which we favor in the absence of any accepted physiological model for *Architeu-*

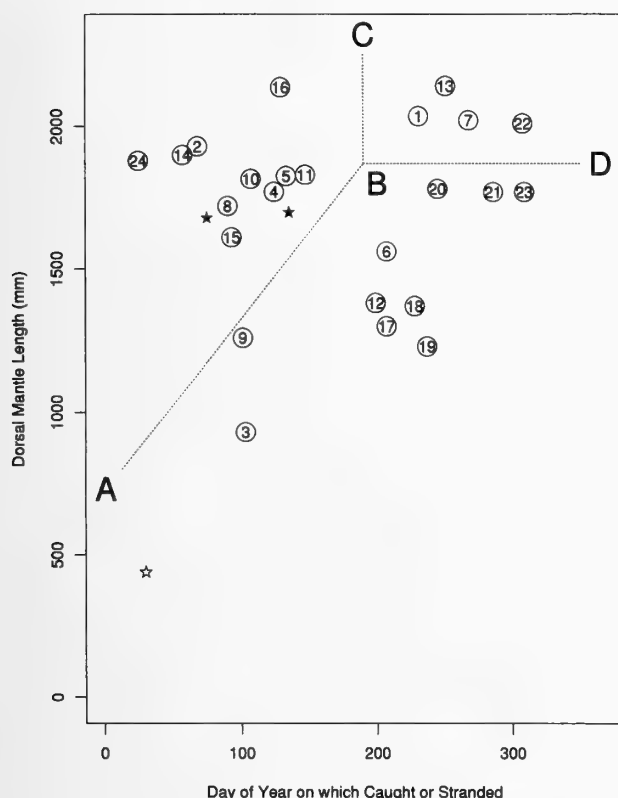


Figure 7

Day of the year of capture plotted against dorsal mantle length for 24 specimens of *Architeuthis kirki* reported in New Zealand waters 1983–1988. The numbers on the figure are the specimen numbers of Table 1 (specimens being ordered by date of capture), and the dotted lines indicate ways of dividing the data assuming that the lifespan of *A. kirki* is between one and three years (see text). The two filled stars on the figure are two *Architeuthis* sp. from South African waters reported by Roeleveld & Lipinski (1991), and the outline star is one *Architeuthis* sp. reported from South Australian waters by Jackson et al. (1991).

this growth. The lowess lines are shown on Figure 8 and Figure 9 and were linearly extrapolated back to give “birthdates” of 1 August in Figure 8 and 2 May in Figure 9.

To allow comparison with previously published cephalopod growth curve studies, we have fitted our data to a range of parametric curves, including the von Bertalanffy growth model,

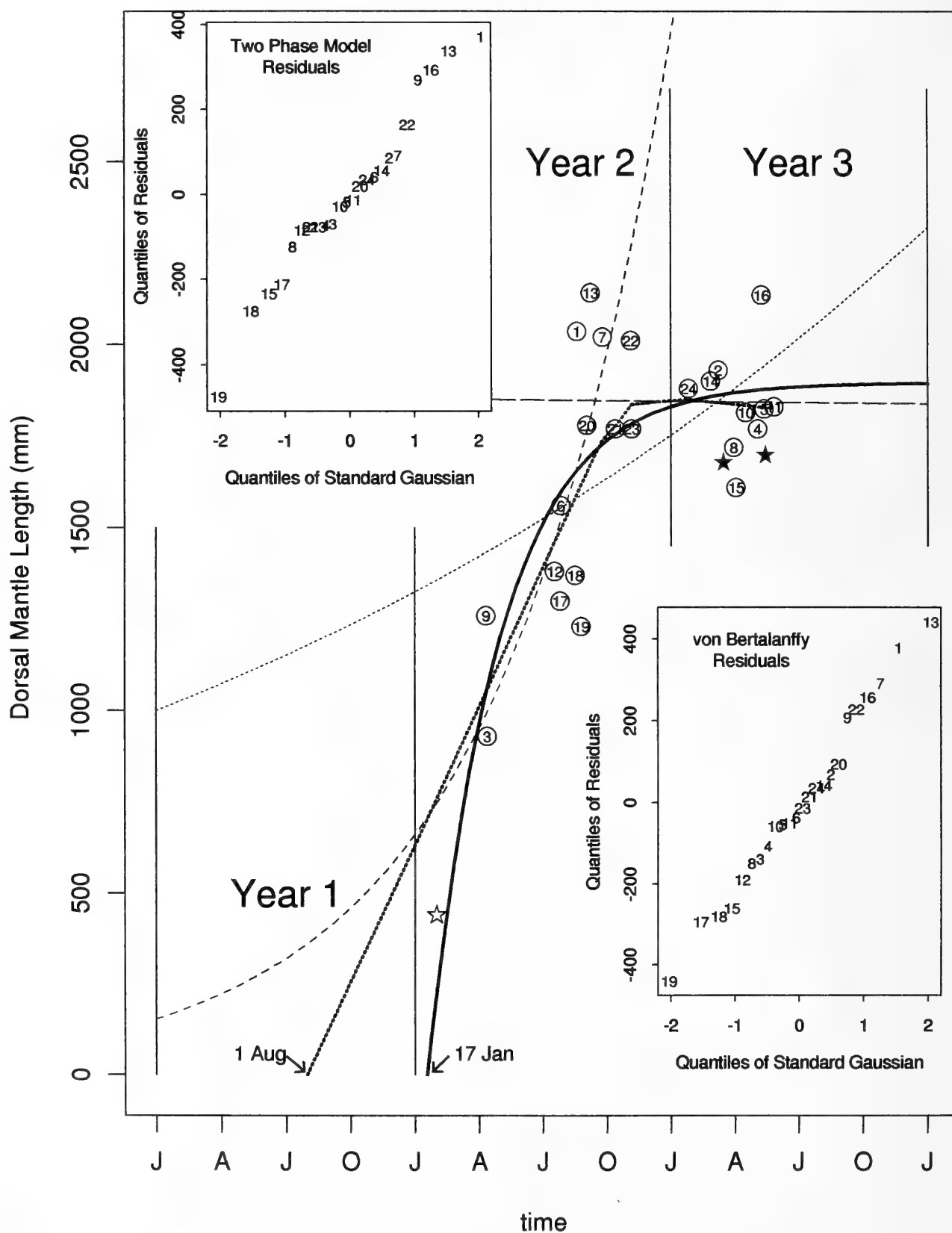
$$l_t = L_\infty(1 - e^{-k(t-t_0)}) \quad [1],$$

where l_t is the DML at time t , and L_∞ , K and t_0 are constant parameters. The estimates of L_∞ , k and t_0 , together with their error estimates, are shown in Table 2. Quantile-quantile (q-q) plots of residuals from the von Bertalanffy model are shown in inserts in Figures 8 and 9. The von Bertalanffy q-q plot for Figure 8 shows a wider spread of residuals than the plot for Figure 9. Two clusters of points are quite distant from the Figure 8 fitted curve: animals 1, 7, 13, and 22 (which are moved one year later in Figure 9) and animals 17, 18, and 19 which were small squid caught in July and August 1987. The jump between residuals 20 and 9 on the von Bertalanffy q-q plot of Figure 8 reflects the outlier nature of animals 1, 7, 13, 16, and 22. Animal 9 also has a high residual, but this is accentuated because the point lies adjacent to the steep part of the curve. A small precocity of growth, or an early birthdate, could easily make this point an outlier. The asymptotic mean maximum length given by the von Bertalanffy model of Figure 8 is 1896 mm; smaller than seven observations in the 24 observation dataset. In the q-q plot of Figure 9, the residuals are more evenly spread about (and much closer to) the von Bertalanffy and lowess lines. The animal groups 1, 7, 13, and 22 and 17, 18, 19 then become much closer to the fitted lines. Animals 15 and 16 are still well away from the fitted lines as was the case in Figure 8. The S shape of the q-q plot of Figure 9 denotes residuals that are from a longer tailed distribution than the Gaussian distribution. The asymptotic DML at 2168 mm is just greater than the longest DML of the dataset.

Exponential and logarithmic growth: A number of workers have argued that it is inappropriate to model

Explanation of Figures 8 and 9.

Time of capture or stranding plotted against dorsal mantle length (DML) for *Architeuthis kirki* reported from New Zealand waters between 1983 and 1988. Figure 8 is constructed by assuming that animals above and to the left of the time ABD on Figure 7 are in their second year of life. Figure 9 is constructed by assuming that animals to the left of the line ABC in Figure 7 are in their second year of life. The heavy dotted curve is a lowess line fit to the data, and the heavy continuous line a von Bertalanffy line fit to the data. The light dotted line is exponential and logarithmic models fitted to all the data. (The two fits give identical curves). The line with the short dashes is an exponential model fitted to points (1, 3, 6, 7, 9, 12, 13, 17, 18, 19, 20) on Figure 8 and the points (3, 6, 9, 12, 17, 18, 19, 20, 21) on Figure 9. The line with the long dashes is a logarithmic model fitted to the points not used to fit the exponential curves in each figure. The two filled stars are specimens from South Africa waters reported by Roeleveld & Lipinski (1991), and the outline star is the specimen from South Australian waters reported by Jackson et al. (1991). The South Africa and South Australian specimens were not used to calculate any of the fitted curves. The inserts show plots of the quantiles of the residuals from the von Bertalanffy line and the two phase exponential-logarithmic line plotted against quantiles of the standard Gaussian (Normal) distribution.



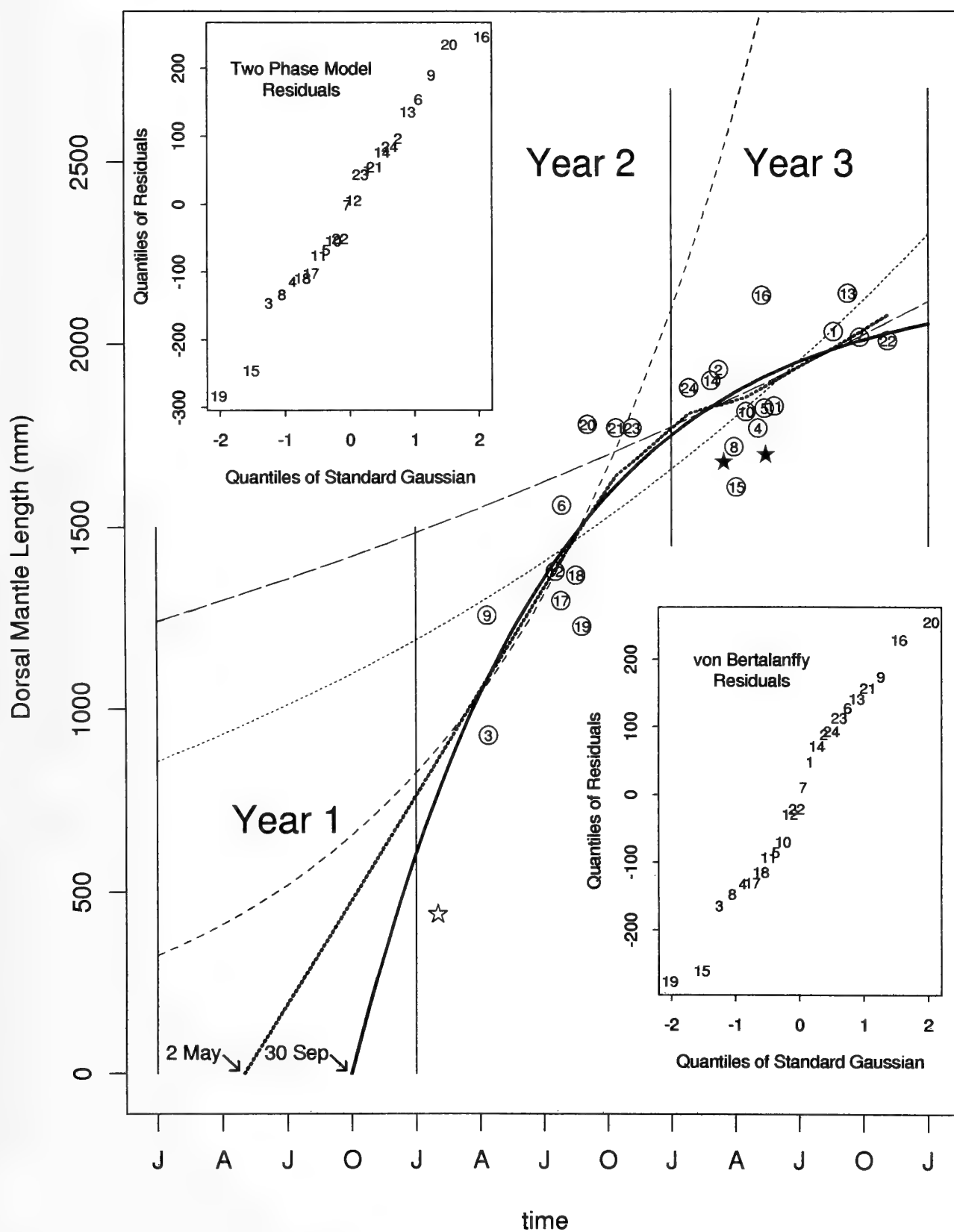


Table 2

Details of the fitting of the lowess, von Bertalanffy and two phase model lines of Figure 8 and Figure 9. The curves are calculated from mantle length in mm and age in days from 1 January in year 1.

Parameter	Figure 8			Figure 9		
	Estimate	Standard error	Residual sum of squares	Estimate	Standard error	Residual sum of squares
Lowess (span = $\frac{2}{3}$, degree = 1)			993,166			462,042
von Bertalanffy			1,124,780			506,018
L_{∞} (mm)	1896	102		2168	213	
k (d^{-1})	0.0097	0.0042		0.0036	0.0017	
t_0 (d)	382	45		273	83	
[from 1 January in year 1]	[17 Jan in year 2]			[30 Sep in year 1]		
Two phase model			691,795			242,240
Phase 1: Exponential						
Animals used	1, 3, 6, 7, 9, 12, 13, 17, 18, 19, 20			3, 6, 9, 12, 17, 18, 19, 20, 21		
a	154.5	121.1		326.4	161.2	
b	0.00399	0.00133		0.00254	0.00085	
Day of transition to logarithmic phase	622			[10 Oct in year 2]		
Phase 2: logarithmic			211,994			212,702
a	1858	409		1242	199	
b	0.9999	0.0003		1.0005	0.0002	

cephalopod growth with functions commonly applied to teleost growth (e.g., see Forsythe & Van Heukelem, 1987; Forsythe & Hanlon, 1989; Jackson & Choat, 1992). A two-phase growth model has been suggested by Forsythe & Van Heukelem (1987), with growth in the first phase being exponential, i.e., described by the equation

$$W = ae^{bt} \quad [2],$$

and growth in the second phase being logarithmic, i.e., described by the equation

$$W = ab^t \quad [3],$$

where W is weight, t is some measure of elapsed time (age), and a and b are constants. It is trivial to show that if weight (w) and dorsal mantle length (l) are related by

$$W = al^b \quad [4],$$

where a and b are constants, and if W and age can be described by the exponential model (equation [2]) or the logarithmic model (equation [3]), then the change in dorsal mantle length over time can also be described by an exponential or logarithmic model. The logarithmic model is sometimes referred to as a "power curve" model.

The two-phase exponential-logarithmic model was fitted by Forsythe & Van Heukelem (1987) and Forsythe & Hanlon (1989) to several species of hatchery reared cephalopods, but they did not discuss how they determined where the transition was made from fitting exponential to fitting logarithmic growth. The laboratory experimenter may have expectations of a change in the nature of growth from knowledge of variations of experimental parameters such as food availability or type, water temperature, or time since hatching. In the absence of such expectations, the point of transition can be determined by adjusting the division of the data points to obtain a best fit according to some predetermined criterion such as minimum residual sum of squares. A minor difficulty arises from the need to ensure that the transition between the two growth curves occurs near the division between the data used to fit each phase. Failure to ensure this can lead to misleading estimates of goodness of fit.

Two-phase exponential-logarithmic models were fitted to the data of Figure 8 and Figure 9. In both Figure 8 and Figure 9, transition points were just below the greatest age point used to fit the exponential section of the curve; 11 days below for Figure 8 and two days below for Figure 9. For both Figure 8 and Figure 9, the residual sum of squares from curve following the exponential curve for ages below the transition point and the logarithmic curve above the transition point is the smallest residual sum of squares of all possible partitions of the data. The residual sums of squares were smaller than those for the corresponding von Bertalanffy curves. The two-phase exponential-logarithmic curves are plotted on Figure 8 and Figure 9, and their estimated parameters are detailed in Table 2. An insert on each of Figure 8 and Figure 9 shows the q-q plots of the residuals of these two phase models.

The two-phase curve closely follows in the von Bertalanffy and lowess curves only in the vicinity of the data, thus similar patterns are seen in q-q plots for all models.

Exponential and logarithmic curves were fitted globally to the data; i.e., the curves were fitted using all the data. For these data the fitted global exponential and logarithmic curves are identical. The global curves are plotted on Figure 8 and Figure 9 and appear as a single line on each figure. They did not fit the data well, with runs of residuals falling below the fitted line, then all above and then almost all below in Figure 8. Figure 9 shows similar runs of residuals.

DISCUSSION

The statocysts of *Architeuthis kirki* were of similar size to the statocysts described in Roeleveld & Lipinski (1991) and Young (1984) and had a similar orientation *in situ*. The internal structure of the statocyst of *A. kirki* differs from the *Architeuthis* described by Young (1984) in that it is divided into an anterior and posterior chamber. Cristae and anticristae were not detectable. In the absence of directly identifiable cristae and anticristae, we have not interpreted the protuberances of the statocysts as hamulae or anticristae. There were 10 protuberances in the statocyst of *A. kirki*, the same number of protuberances in *Architeuthis* sp. illustrated by Young (1984: pl. 7, fig. 91(b)) and by Roeleveld & Lipinski (1991).

The semicircular canals analogy in squid has been described in some detail by Stephens & Young (1978). Our three-dimensional model (Figure 2) showed four possible chambers within the statocyst. Two of those chambers have three possible fluid movement exit/entrances, and the other two chambers (the most anterior and posterior) have only two exit/entrances. The consequent interconnections are shown diagrammatically in Figure 3C. The combination of "ampullae" provided by the chambers of the statocyst, and the "canals" by the fluid movement exit/entrances, means that there are organizationally two semicircular canals, slightly tilted with respect to each other, but more or less vertically placed in the dorso-ventral plane with the statolith occupying a chamber at the anterior end. One of the problems with the interpretation of the statocyst as an analogue to the teleost labyrinth is subjectivity in deciding the critical point of how fluid flow may be constrained from chamber to chamber. More combinations of canals may be possible, but the presence of three interconnected chambers jointly connected to the chamber of the statolith admits two effective "semicircular canals" as the most economic solution. The value calculated for the Jones & Spells (1963) statistic is low compared to fishes, but is in the range of many terrestrial vertebrates (Jones & Spells, 1963). The relatively low sensitivity of the squid "labyrinth" to angular acceleration may reflect its relative crudity as an anatomical structure, because the leaky "canals" would require wide bores, low "canal" radii, and large "ampulla" volumes in order to function at all. Two

"semicircular canals" would place *Architeuthis kirki* at the same level of functional sensitivity as the lamprey. The vestibule of the inner ear of the lamprey is divided by a sill into two general cavities reminiscent of the overall structure of the statocyst of *A. kirki*. However, although the lamprey labyrinth has two well-defined semicircular canals, their function may involve directing the flow of fluids over the ciliated surface of the two general cavities (Lowenstein et al., 1968). Therefore, a combination of directed flow in two directions over the sill of the statocyst may provide a crude but effective analogue of the lamprey inner ear that retains the essential requirement of directed turbulence of fluids that is central to labyrinth function.

In arguing convergence, it must be remembered that the issue is convergence of function as well as form. The three semicircular canals of the teleost relate to a complex system of fins and attendant muscles that can control the three-dimensional orientation of the fish. Because the mouth of the fish is at the anterior, it is necessary for teleosts to have developed three-dimensional control both in terms of fins and semicircular canals in order to direct the anterior mouth accurately at this target. Squid acquire their prey by highly extended tentacles that seize and direct prey to its mouth. Squid, in contrast to fish, have very little three-dimensional control, having only a pair of opposed fins in the same plane. A well-developed system of three semicircular canals would therefore be of little use to the squid as it has no means to use the information that such a structure provides. It is more reasonable to see squid as at the same level of stability control as the jawless fishes and therefore possibly convergent on a relatively simple inner ear structure that is consistent with limited levels of control of body orientation in three-dimensional space.

The general morphology of the statolith is similar to that of many other squid species (Clarke, 1978). Both the crystals observed in the body of the otolith and the long monoclinic crystals observed on the surface have also been described in statoliths of other squid species (Clarke, 1978). However, the kind of crystal organization shown in Figure 3C, D and E is atypical of teleosts. Deposition of surface crystals that are absorbed into, or cemented over, by the main crystallized body has been observed in the otoliths of fishes less advanced than teleosts. For example, the lungfish *Neoceratodus forsteri* (Gauldie et al., 1986) and the sturgeon *Acipenser* sp. (Carlstrom, 1963) showed crystalline aggregate otoliths with crystal resorption. Chimaeras also showed a tendency for the small otoconia of the inner ear to fuse into massive structures (Gauldie et al., 1987).

Sections of the statolith of *Architeuthis kirki* have a similar appearance to those of the other squid (Radtke, 1983; Lipinski, 1986), both in terms of microincrement width and orientation, and the presence of check-like structures. We counted microincrements on the basis of their desorption as daily periodic structures in other species (Kristensen, 1980; Hurley et al., 1983; Morris & Aldrich, 1984). The appearance of checks on the tissue-facing side of the

statolith appears to result from fusion of microincrements and is similar to checks observed in vertical sections of some teleost otoliths (Gauldie, 1990).

A wide variety of growth curves has been reported for squids, e.g., Boyle (1990: fig. 2) for *Loligo* sp. It has been argued by Boyle (1990) that cephalopod growth is either slowed drastically or becomes erratic at the onset of sexual maturity. For species with a short breeding season, this point of slow growth might be reached simultaneously at the same age and at the same body size by the bulk of the population. In other species, sexual maturity occurs over a very wide range of body sizes. Growth also appears to vary widely from season to season (e.g., Hatfield (1991) for *Loligo gahi*), and from individual to individual of the same brood when ample food is available (Hurley (1976) and Yang et al. (1986) for *Loligo opalescens*). Young squid are capable of dramatically fast, exponential growth when food is not limiting (Yang et al., 1986). Asymptotic mantle size as a function of time has been observed in wild population, e.g., Natsukari et al. (1988) for *Photoligo edulis*, Spratt (1978) for *Loligo opalescens*, Patterson (1988) for *Loligo gahi* (although no evidence of any asymptotic growth was found for the *Loligo gahi* by Hatfield (1991)), and for *Illex argentinus* (Hatanaka (1986)). Linear, logarithmic, or exponential growth has been reported by Hurley (1976), Turk et al. (1986), Yang et al. (1986), and Hatfield (1991) for *Loligo opalescens*, for *Loligo vulgaris*, and for *Loligo opalescens*, all hatchery reared animals where presumably there was no food limitation or temperature fluctuation. It has been argued that there is no evidence to justify modeling individual squid growth with models that imply growth to an asymptotic size, such as the von Bertalanffy growth model (Forsythe & Van Heukelem (1987), Saville (1987), Forsythe & Hanlon (1989), Rodhouse & Hatfield (1990b) and Jackson & Choat (1992)). However, most of the data advanced to support the absence of asymptotic growth has been from laboratory studies (Forsythe & Van Heukelem, 1987; Forsythe & Hanlon, 1989) or from field studies where the authors have acknowledged that their fishing gear may not have captured the largest individuals (Jackson & Choat, 1992). In their study of hatchery reared *Loligo forbesi*, Forsythe & Hanlon (1989) reported exponential growth for approximately the first 100 days followed by logarithmic growth or exponential growth beyond 100 days. We think that it is unlikely, from the evidence presented by the lowest and von Bertalanffy curves, and from microincrement counts in the statolith of the South Australian specimen (Jackson et al., 1991), that any of the New Zealand specimens of *Architeuthis kirki* were as young as 100 days. However, we were unable to get a good fit to the length-at-age data using a single exponential or single logarithmic function as, for example, Forsythe & Hanlon (1989) claim for *Loligo forbesi*. We could, however, get good fits to segments of the data. This suggests that the reasonable fit obtained by the two-phase exponential-logarithmic model might be because the two-phase model acts as a simple locally weighted model, not because

of the parametric nature of the two-phase exponential-logarithmic model. This reinforces our preference (in the absence of an accepted physiological model) for a non-parametric locally weighted method of curve fitting. However, the apparent asymptotic growth seen in size-at-time data for wild populations may simply arise from Lee's phenomenon (Ricker, 1975) in which large, faster growing squid mature, spawn, and die in advance of slower growing members of their cohort.

The length-at-time-of-reporting data for the 24 *Architeuthis kirki* reported around New Zealand in the period 1983–1988 do not and cannot yield unambiguous information on growth. If *A. kirki* have a life cycle less than 2.5 years, a defined breeding season, and similar growth rates over the years 1983–1988, then all of curves, lowess, von Bertalanffy, and two-phase exponential-logarithmic curves, may be used to represent growth. Two *Architeuthis* sp. reported from South Africa by Roeleveld & Lipinski (1991) and one from South Australia reported by Jackson et al. (1991) are also shown on Figure 8 and Figure 9, and their ages agree well with both lowess and von Bertalanffy curves.

The regular distribution of the residuals from the von Bertalanffy curve of Figure 9 and the position of the asymptote relative to known mantle sizes inclines us to favor the curves of Figure 9. The estimate of the parameter k for Figure 9 was 0.0036d^{-1} and corresponds to the values of 0.0030d^{-1} (males) and 0.0031d^{-1} (females) estimated by Hatanaka (1986) for the small temperate water squid *Illex argentinus*. The high value of k may also reflect the rapid development rate necessary for squid because of their short life span (Beverton & Holt, 1957, p. 288). The statolith of an *Architeuthis* sp. caught on 30 January 1982 off South Australia was reported by Jackson et al. (1991) to have 153 microincrements. If such microincrements were deposited daily, then the animal would have a putative birth date of 30 August 1991, which accords well with the von Bertalanffy curve of Figure 9. A review of whether microincrements are deposited daily in several species of squid can be found in Rodhouse & Hatfield (1990b). The statolith described in this paper, which was collected off New Zealand on 3 May 1987, had 393 microincrements. This would give a putative birth date of 6 April 1986. This does not accord well with any of the curves we have presented and suggests that early growth is much more rapid than either the lowess curve or the von Bertalanffy curve suggests. The birth date of the South Australian specimen diverges widely from the two-phase model. In the lowess and von Bertalanffy, the implied early growth rate is high and growth to 1.6 meters mantle length in a little over a year appears unexceptional. The tissues of the squid mantle are highly collagenous and what little skeleton is present is in the form of cartilage. Both cartilage and collagen have very low energy demands (less than 1% of that of bone), and the consequent energy conversion efficiency of squid may be high. Very rapid early growth would explain why so few small specimens of *Architeuthis*

sp. have been reported. In order to solve these uncertainties, it is important that all specimens of *Architeuthis* captured, especially small specimens, are reported and that statoliths are obtained and stored dry wherever possible.

Giant squid are rarely available for scientific study. Consequently, details of their life history become known slowly through examination of what are usually small numbers of individuals. The flexible growth curve estimation method described here allows small sets of size and time-of-catch data (which are often the only data available) to be added progressively to provide an increasingly robust estimate of growth rate. Hopefully, more statoliths will be collected, allowing more alternative estimates of growth rate, particularly for small specimens.

The absence in the cephalopod literature of widely discussed quantitative physiological models of growth makes the rational choice of a parametric weight-at-age or a length-at-age curve very difficult. In the absence of such models, we note that the non-parametric lowess curves essentially follow the von Bertalanffy and two-phase exponential-logarithmic curves for *Architeuthis kirki*, without requiring the parametric assumptions of either von Bertalanffy or the two exponential-logarithmic models. In the absence of accepted physiological models of cephalopod growth, we advocate the wider use of lowess curves.

ACKNOWLEDGMENTS

We thank Kevin Mulligan and Alan Blacklock of the Marine Research Center, Greta Point, New Zealand, and Brooks Bay of SOEST Publication Center for their technical and photographic expertise. This is SOEST contribution no. 3325.

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Review of the Type Species of *Lirobarleeia* Ponder, 1983

by

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Abstract. Ponder (1983:243) designated *Alvania galapagensis* Bartsch, 1911, as the type species of the genus *Lirobarleeia* Ponder, 1983. The species figured by Ponder (1983:264, fig. 12A–D) is not *A. galapagensis* Bartsch, 1911. *Lirobarleeia galapagensis* of Ponder, 1983, is herein put in synonymy of *Lirobarleeia nigrescens* Bartsch & Rehder, 1939. *Lirobarleeia nigrescens* is compared to two similar species from Islas Galápagos, *Lirobarleeia galapagensis* (Bartsch, 1911) and *Alvinia halia* (Bartsch, 1911).

INTRODUCTION

Ponder (1983) established the genus *Lirobarleeia* based on his study of a number of Barleeidae species. He established the type of the genus as *Alvania galapagensis* Bartsch, 1911, since his anatomical studies were conducted on what he believed to be specimens of *A. galapagensis*. Ponder (1983:264, fig. 12A–D) figured scanning electron microscope (SEM) photographs of shell, radula, operculum, and protoconch of a species identified as *Lirobarleeia galapagensis* (Bartsch). The shell, protoconch, and operculum were of a specimen from Bahía Academy, Isla Santa Cruz, Islas Galápagos (AMS C.137206, ex LACM 66-120), and the radula figured was of a specimen taken between Pta. Tomayo and Bahía Academy, Islas Galápagos (AMS C.137207, ex LACM 66-119).

While working on a large collection of micromollusks collected by Kirstie L. Kaiser on the 1988 Grupo Victoria Expedition to the Islas Galápagos, I came across a lot of specimens that appeared to be the species figured by Ponder (1983) as *Lirobarleeia galapagensis*. Ponder's figures (1983:figs. 12A, D) differ from *Alvania galapagensis* described and figured by Bartsch (1911:347–348, pl. 30, fig. 9). A scanning electron micrograph of the holotype (USNM 207590) of *A. galapagensis* is shown in Figure 1, and differs from the specimen used by Ponder for the type species of *Lirobarleeia* (shown here, with permission of the Australian Museum, as Figures 2 and 3). The question then arose as to the real identity of the specimen of *L. galapagensis* of Ponder, 1983.

MATERIALS AND METHODS

This review is hampered by the scarcity of specimens of *Alvania galapagensis* Bartsch, 1911. In contrast, many lots

of *Lirobarleeia galapagensis* of Ponder, 1983, approximately 800 specimens, were studied. Freshly collected material studied here was collected by K. L. Kaiser in the Grupo Victoria Expedition to the Islas Galápagos. SEM photographs of uncoated specimens at 2 KV were taken of the holotypes of *A. galapagensis* Bartsch, 1911, *Alvania nigrescens* Bartsch & Rehder, 1939, and a similar looking Galapagan species, *Alvania halia* Bartsch, 1911. These high magnification photographs were used to study shell microstructure.

Institutional abbreviations are as follows: AMS, Australian Museum, Sydney; LACM, Los Angeles County Museum of Natural History; and USNM, National Museum of Natural History, Smithsonian Institution.

SYSTEMATICS

RISSOOIDEA Gray, 1847

BARLEEIDAE Gray, 1857

Lirobarleeia Ponder, 1983

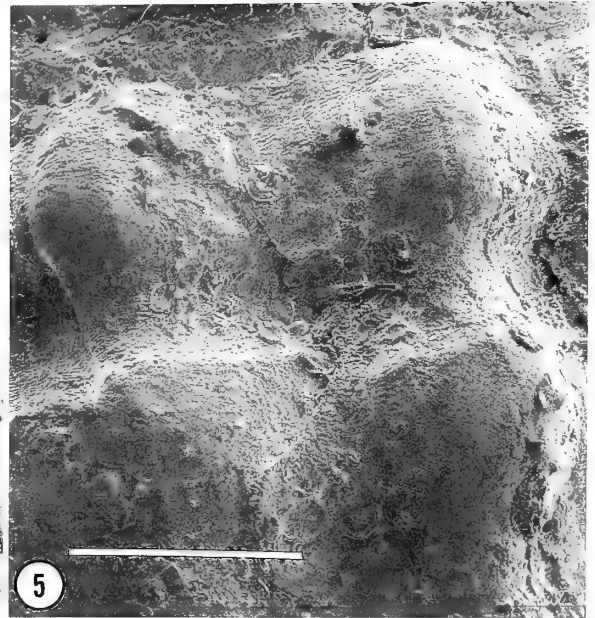
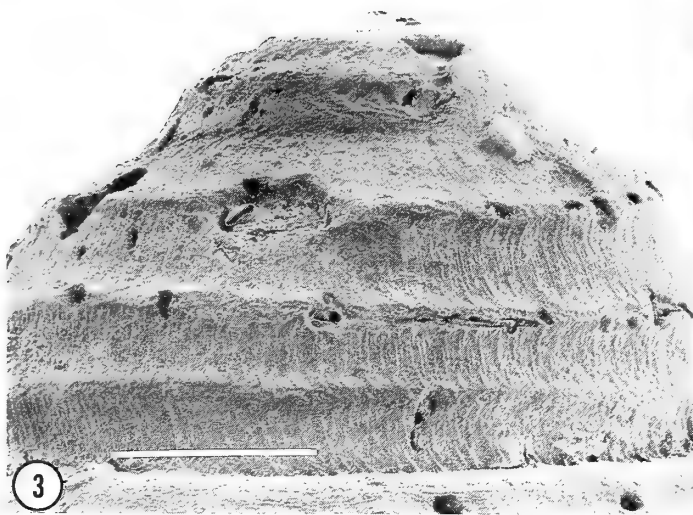
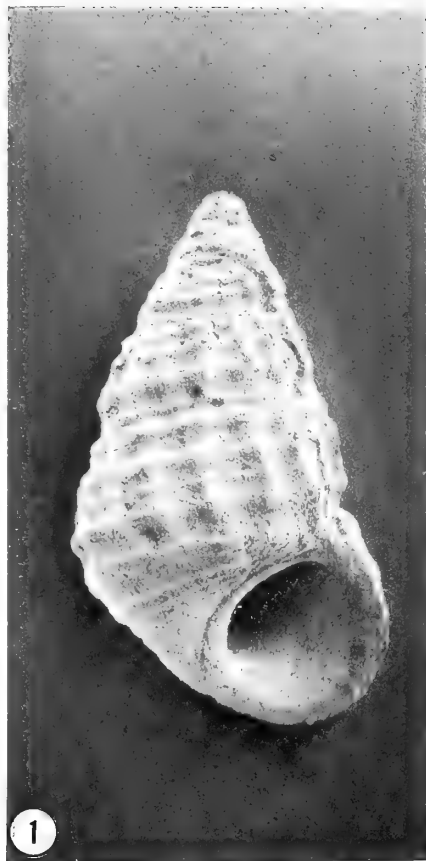
Type species: *Alvania galapagensis* Bartsch, 1911, of Ponder, 1983, not Bartsch, 1911 [= *Lirobarleeia nigrescens*, Bartsch & Rehder, 1939]

Lirobarleeia nigrescens (Bartsch & Rehder, 1939)

(Figures 2–11)

Alvania nigrescens Bartsch & Rehder, 1939:8, pl. 2, fig. 5.
Lirobarleeia galapagensis (Bartsch): Ponder, 1983:243–244, fig. 12A–D.

Background: *Alvania nigrescens* was described and figured from a single specimen by Bartsch & Rehder (1939:8,



Explanation of Figures 1 to 5

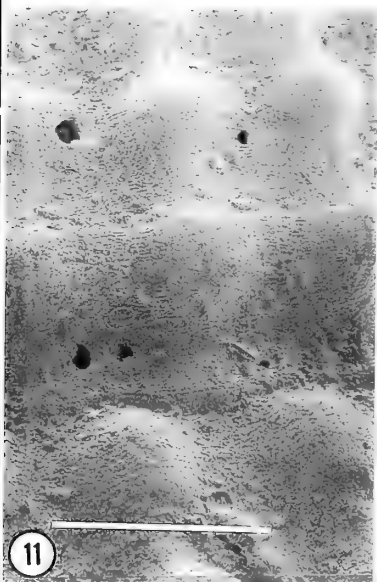
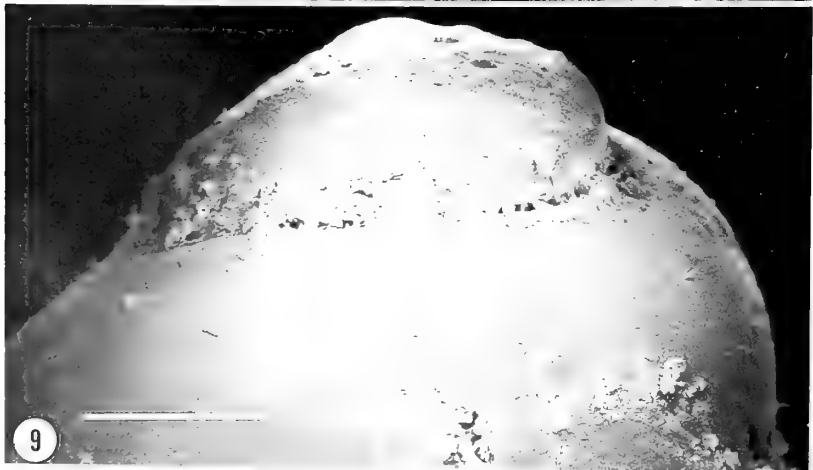
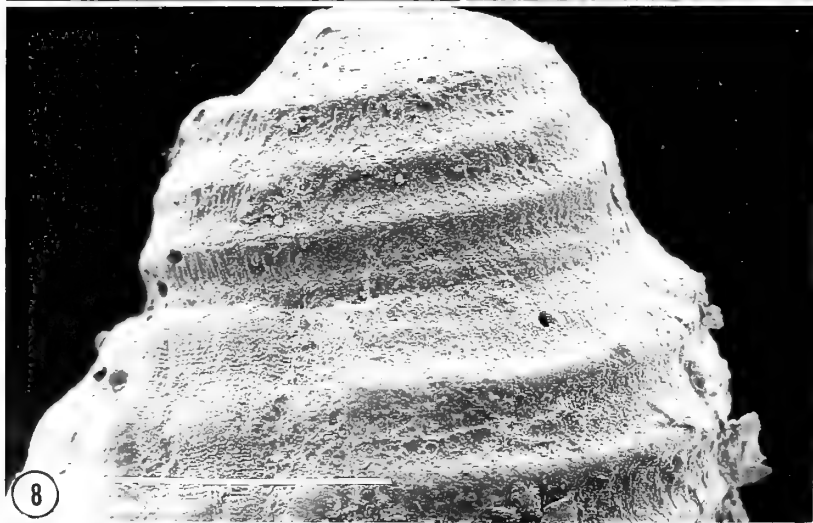
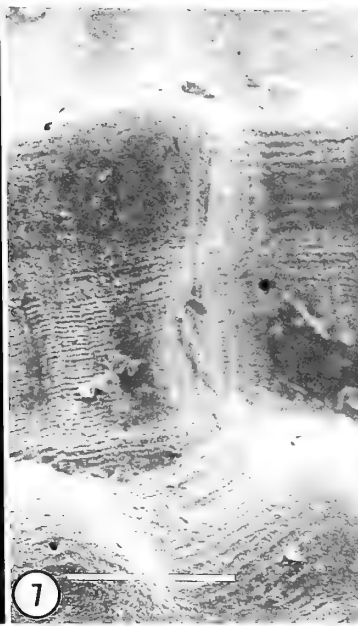
Figure 1. SEM photograph of holotype of *Alvania galapagensis* Bartsch, 1911 (USNM 207590), Length = 3.1 mm.

Figure 2. *Lirobarleeia galapagensis* of Ponder, 1983, specimen from Bahía Academy, Isla Santa Cruz, Islas Galápagos (0°44.5'S, 90°18.5'W) (AMS C.137206, ex LACM 66-120). From Ponder (1983:264, fig. 12A), reprinted with permission of the Australian Museum, Sydney. Length = 3.3 mm.

Figure 3. Protoconch of specimen shown in Figure 2. From Ponder (1983:264, fig. 12D), reprinted with permission of the Australian Museum, Sydney. Scale bar = 100 μ m.

Figure 4. SEM photograph of holotype of *Alvania nigrescens* Bartsch & Rehder, 1939. Length = 3.1 mm.

Figure 5. Microsculpture of specimen shown in Figure 4. Scale bar = 200 μ m.



pl. 2, fig. 5). The holotype (USNM 472621) is elongate-conic, chestnut brown, and approximately the same size (length 3.1 mm, diameter 1.5 mm) as *Lirobarleeia galapagensis* of Ponder, 1983. The dead specimen of *A. nigrescens* was collected "in a tide pool" on Old Providence Island, Caribbean Sea (Isla de Providencia, Colombia) by Dr. Waldo L. Schmitt, Curator of the Division of Marine Invertebrates of the United States National Museum, on the Presidential Cruise of 1938. Ponder (1983:244) synonymized *A. nigrescens* with *L. galapagensis* of Ponder, 1983, and stated that "the West Indian locality for this last name is erroneous." I agree with Ponder that *A. nigrescens* is a Galapagan species and not Caribbean. The type lot has a series of labels, all stating the collecting data reported by Bartsch & Rehder (1939:8). However, Waldo Schmitt on the Presidential Cruise of 1938 collected extensively in the Islas Galápagos in June and July of 1938, prior to collecting at Isla de Providencia (6 August 1938), and I believe the locality data of the holotype of *A. nigrescens* was later confused during curation. In over 50 years no additional specimens matching the description of *A. nigrescens* have been found in the Caribbean, although the isolated Isla de Providencia may not have been subsequently collected.

Species description: On the basis of examining approximately 800 specimens as well as SEM photographs of shell microstructure, a revised description of the shell of this species is given as follows. Length 3.0–3.5 mm, diameter 1.5–1.8 mm, reddish-brown, elongate-conic, solid. Protoconch of 2–2½ well-rounded whorls with random irregularly shaped pits, having three poorly defined spiral lirations and axial growth lines between spirals. Teleoconch of approximately four whorls, with well-defined suture, both spiral and axial sculpture with spiral cords dominant. Whorls shouldered at summit, 14 strong axial ribs on early whorls, 16 on penultimate, and 18 on body whorl; ribs extending strongly from summit of whorl to suture. Whorls marked by three strong spiral cords, the first occurring at angle of shoulder near summit, the second on middle of whorl and the third immediately above suture; many fine, wavy, spiral lirations paralleling major spiral cords. Posterior spiral cord weak on earliest whorls and

increasing in strength, becoming strong on penultimate whorl. Intersections of axial ribs and spiral cords forming strong tubercles and clathrate sculpture; tubercles sloping anteriorly forming concave surfaces, spaces between tubercles forming deeply impressed squarish pits, occasional fine spiral thread in sutures of whorls. Basal area non-umbilicate, attenuated anteriorly, somewhat concave. Base bounded by strong peripheral cord; a partially noded cord immediately anterior to the peripheral cord and four strong, smooth cords that grow progressively weaker and closer spaced from the periphery to the umbilical region. Rounded aperture with simple peristome; outer lip thickened by external varix; inner lip appressed to base. Posterior spiral cord of body whorl having an inverted V-shaped build-up of material immediately above posterior portion of aperture.

Distribution: Islas Galápagos, Ecuador.

Specimens examined: In addition to the type lot, I examined approximately 800 specimens from 28 lots. Eight lots were from the K. L. Kaiser collection, two from the AMS, and 18 from the LACM. All specimens were from the Islas Galápagos and were collected from the intertidal to a depth of 101 m. A majority of the shells were collected intertidally. Shells examined were from, or waters nearby, the following islands: Isla Santa María (Floreana, Charles), Isla Española (Hood), Isla Seymour, Isla San Salvador (Santiago, James), Isla Santa Cruz (Indefatigable), Isla Bartolomé, Isla Genovesa (Tower), Isla Pinta (Abingdon), Isla Fernandina (Narborough), Isla Isabela (Albemarle), and Isla Baltra (South Seymour).

Discussion: *Lirobarleeia nigrescens* is the most common *Lirobarleeia* in the Islas Galápagos but apparently has been misidentified in the past because of its general similarity to *Alvania galapagensis* Bartsch, 1911. *Alvania galapagensis* is a deep-water species that is more pear shaped, having more flattened and widely separated nodes, and less channeled sutures than *L. nigrescens*. The latter is dark reddish-brown but much of the material examined was eroded or sun-bleached, and therefore many of the specimens examined were varying shades of light brown, orange, and yellow; in one lot there were three colorless shells (LACM

Explanation of Figures 6 to 11

Figure 6. SEM photograph of *Lirobarleeia nigrescens* (Bartsch & Rehder, 1939) specimen collected by K. L. Kaiser (LACM 148956), at Punta Cormorant, Isla Santa María, Islas Galápagos (1°13'S, 90°26'W). Length = 3.1 mm.

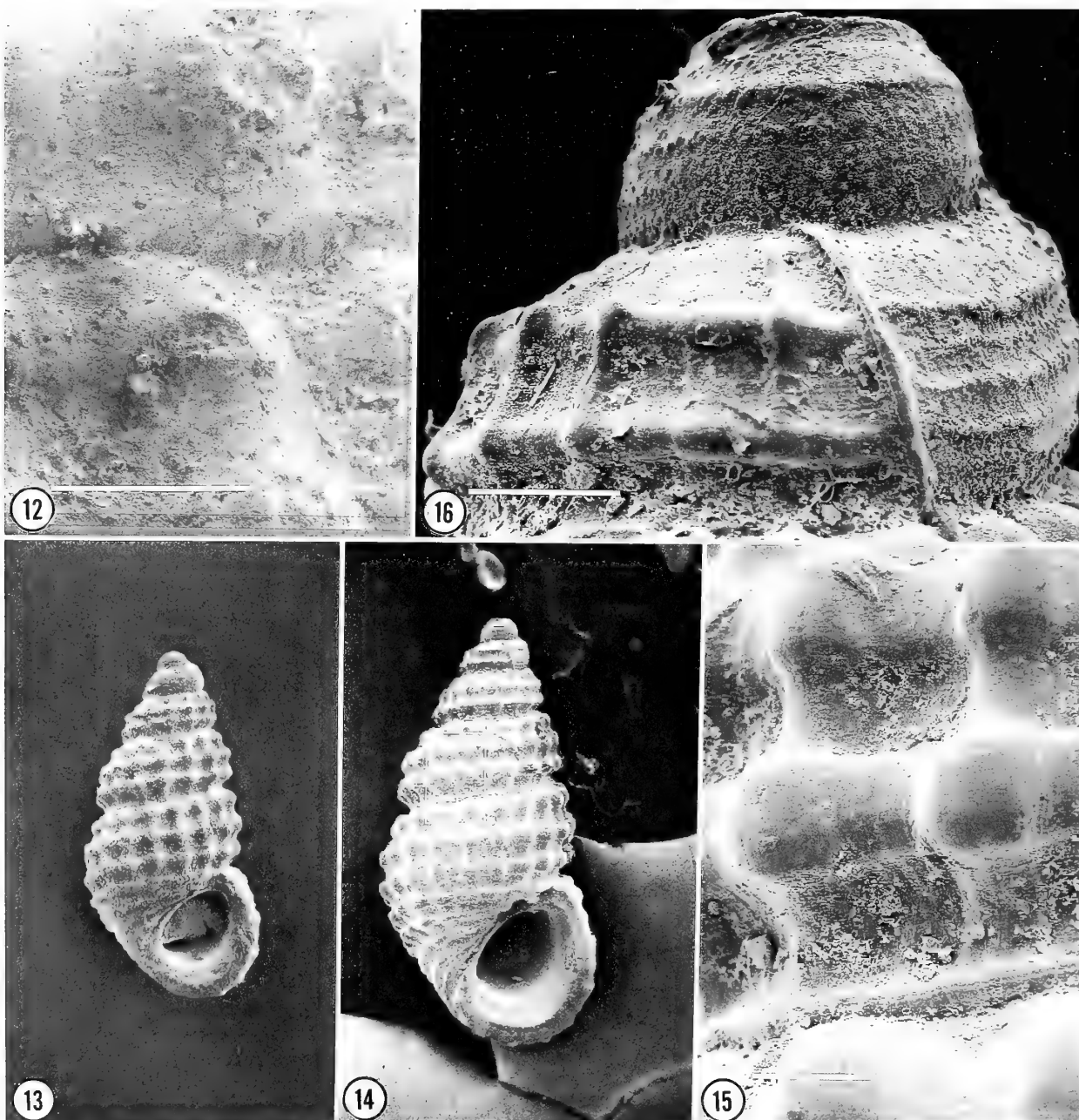
Figure 7. Enlarged detail of sculpture enclosed in rectangular box in Figure 6. Scale bar = 125 µm.

Figure 8. SEM photograph of protoconch of *L. nigrescens* specimen collected by K. L. Kaiser (LACM 148957), at Jimmy's Reef, N side Isla Española, Islas Galápagos (1°21'S, 89°39'W). Scale bar = 200 µm.

Figure 9. SEM photograph of protoconch of *L. nigrescens* specimen shown in Figure 6, collected at Punta Cormorant, Isla Santa María, Islas Galápagos. Scale bar = 100 µm.

Figure 10. SEM photograph of *L. nigrescens* specimen (LACM 66-119) collected between Punta Tomayo and Bahía Academy, Islas Galápagos (0°47.7'S, 90°20.5'W). Length = 3.5 mm.

Figure 11. Microsculpture of specimen shown in Figure 10. Scale bar = 200 µm.



Explanation of Figures 12 to 16

Figure 12. Microsculpture of holotype of *Alvinia galapagensis* Bartsch, 1911. Scale bar = 200 μ m.

Figure 13. SEM photograph of holotype of *Alvinia halia* Bartsch, 1911. Length = 2.3 mm.

Figure 14. SEM photograph of *Alvinia halia* (Bartsch, 1911) specimen collected by K. L. Kaiser (LACM 148958), at Devil's

Crown, Isla Santa María, Islas Galápagos (1°12'S, 90°25'W). Length = 2.3 mm.

Figure 15. Enlarged detail of sculpture enclosed in rectangular box in Figure 14. Scale bar = 125 μ m.

Figure 16. SEM photograph of protoconch of specimen shown in Figure 13. Scale bar = 100 μ m.

84-47). A large number of the examined specimens appeared to have the protoconchs eroded smooth and rounded as shown in Figure 9 in contrast to the protoconchs with spirals as shown in Figures 3 and 8. Figure 8 is an SEM

photograph of a *L. nigrescens* specimen collected by K. L. Kaiser having a much less eroded protoconch (collected at Jimmy's Reef, N side Isla Española, Islas Galápagos in 17 m, 16 February 1988, among lava rock and coarse sand),

and it shows four spiral cords on the protoconch with the axial growth lines and random pits. A large number of juvenile specimens examined (LACM 84-39) had more-defined, fine spiral sculpture. Many of the adult specimens examined had a beige coating on the protoconch and early teleoconch whorls, and where the coating was eroded or chipped away the protoconch appeared smooth and rounded. In one case, a specimen (LACM 72-196) was observed with spiral sculpture locally eroded, exposing a smooth and rounded underlayer. There is some variation in body sculpture, with occasional specimens having stronger axial ribs spaced farther apart. Many specimens lack a thread in the sutures, and the basal areas have varying degrees of concavity. In some cases the aperture is not quite round, occasionally having a squared look.

Lirobarleeia nigrescens is closest in external sculpture to two other Galapagan species: *L. galapagensis* and *Alvinia halia* (Bartsch, 1911).

Lirobarleeia galapagensis (Bartsch, 1911)

(Figures 1, 12)

Alvania galapagensis Bartsch, 1911:347-348, pl. 30, fig. 9.

Alvinia (Alvinia) galapagensis: Keen, 1971:368, fig. 196; Finet, 1985:13.

Lirobarleeia galapagensis: Shasky, 1989:9; Finet, 1991:269.

Remarks: *Lirobarleeia galapagensis* (Bartsch, 1911) is from deeper water, 1160 m (634 fm), whereas *L. nigrescens* has been found from the intertidal down to 101 m. I considered the possibility that *L. galapagensis* was a deep-water eco-phenotype of *L. nigrescens* but rejected it for the following significant differences. The type lot (holotype and two paratypes) of *L. galapagensis* (USNM 207590) are ovate shells, yellow-white, and have a larger diameter for similar length shells than the elongate-conic, dark reddish-brown specimens of *L. nigrescens*. The holotype measurements reported by Bartsch (1911) were length 3.3 mm and diameter 1.9 mm, but recent measurements give a length of 3.1 mm and a diameter of 1.8 mm. The two paratypes are identical in appearance to the holotype, and each has a length of 2.8 mm. The predominant sculpture of *L. galapagensis* is the axial ribs, in contrast to the spiral cords of *L. nigrescens*. In *L. galapagensis* the teleoconch whorls are less shouldered and the sutures not as depressed as in *L. nigrescens*. *Lirobarleeia galapagensis* has a fourth spiral cord, which appears between the middle and anterior spiral cords on the penultimate whorl and continues on the body whorl, whereas *L. nigrescens* has three spiral cords on all whorls. *Lirobarleeia nigrescens* is closer in shell characteristics to another Galapagan species, *Alvinia halia* (Bartsch, 1911), than to *L. galapagensis*. There have been no anatomical studies of *L. galapagensis*, since it is known from the type lot only. Therefore, generic placement for this species remains questionable. Figure 12 is an SEM photograph of the microstructure of the holotype of *L. galapagensis*, and it shows the same spiral striations as in *L. nigrescens*. The protoconchs of the holotype and paratypes

of *L. galapagensis* are too worn to use as indicators for generic placement.

Distribution: Islas Galápagos, Ecuador.

Specimens examined: Type lot (USNM 207590: holotype plus two paratypes).

RISSOIDAE Gray, 1847

Alvinia Monterosato, 1884

Type species: *Alvania weinkauffi* (Mohrenstern ms) Weinkauff, 1868; subsequent designation Crosse, 1885.

Alvinia halia (Bartsch, 1911)

(Figures 13-16)

Alvania halia Bartsch, 1911:354-355, pl. 31, fig. 5.

Alvinia (Alvinia) halia: Keen, 1971:368; Finet, 1985:13.

Manzonina (Alvinia) hiala [sic]: Ponder, 1985:48.

Lirobarleeia halia: Shasky, 1989:9; Finet, 1991:269 (Shasky erroneously cites Ponder [1983] for this change).

Background: Many *Alvinia* species appear similar to those of *Lirobarleeia*, both having small shells of similar shape, a duplicated peristome, and clathrate sculpture. Although Ponder (1985:48) placed *Alvinia* as a subgenus of *Manzonina*, his justification for doing so was not strongly argued. The protoconch of *Alvania* differs significantly from that of *Lirobarleeia* (Figures 3, 16), and there are significant anatomical, opercular, and radular differences. However, in the case of *Alvinia halia*, there have been no anatomical studies. The protoconch and duplicated peristome of *A. halia* are similar to those of *A. weinkauffi* (see Ponder, 1985:151, figs. 102A, B), the type species of *Alvinia*.

Remarks: Shells of the type lot (holotype and 15 paratypes) of *Alvinia halia* (USNM 195000) are elongate-conic, white, somewhat eroded, and smaller (holotype: length 2.3 mm, diameter 1.1 mm) than the dark reddish-brown specimens of *Lirobarleeia nigrescens*. Figure 13 is an SEM photograph of the holotype. An SEM photograph of a non-eroded specimen of *A. halia* collected by K. L. Kaiser on the Grupo Victoria Expedition to the Islas Galápagos is shown in Figure 14. The specimens from this lot varied in length from 2.3 to 2.4 mm and had approximate diameters of 1.1 mm. The overall sculpture of *A. halia* is similar to that of *L. nigrescens*, having a protoconch of 1½ whorls and four teleoconch whorls, three spiral cords per whorl, and approximately the same number of axial ribs. However, *A. halia* is smaller, more slender, and has more pronounced and deeper sutures than *L. nigrescens*. In comparing Figures 5 and 15, *A. halia* shows only traces of the fine, wavy, spiral striae (at high magnification) that parallel the major spiral cords in *L. nigrescens*. Figure 16 is an SEM photograph of the protoconch of the specimen of *A. halia* shown in Figure 14. The protoconch of *A. halia* has four spiral cords and is papillose; it lacks the axial growth lines between axial cords and has smaller and fewer random irregular pits than *L. nigrescens*. The first teleo-

conch whorl of *A. halia* is more shouldered and has narrower, stronger axial ribs, which result in sharper, more pronounced tubercles than those of *L. nigrescens*.

Distribution: Islas Galápagos, Ecuador.

Specimens examined: Type lot (holotype and 15 paratypes), 73 m; Devil's Crown, Isla Santa María (Floreana) (1°12'S, 90°25'W), in 9–12 m, 14 February 1988, 8 specimens, K. L. Kaiser leg; Plaza Norte, Isla Santa Cruz (0°35'S, 90°10'W), in 11 m, 13 February 1988, 17 specimens, K. L. Kaiser leg.

CONCLUSIONS

Ponder's (1983) designated type species for the genus *Lirobarleeia* was erroneously identified as *Alvania galapagensis* Bartsch, 1911, a species different from the one he used for his anatomical and morphological studies. *Lirobarleeia galapagensis* of Ponder, 1983, becomes a synonym of *L. nigrescens* (Bartsch & Rehder, 1939), a species named from a single specimen reportedly collected in the Caribbean. No additional specimens of *L. nigrescens* have been collected in the Caribbean in over 50 years and it is believed that the Islas Galápagos is the true type locality for *L. nigrescens*.

Since Ponder's extensive anatomical studies to support the creation of the genus *Lirobarleeia* were all conducted on specimens of *L. nigrescens* = *L. galapagensis* of Ponder, 1983, it seems appropriate that *L. nigrescens* be specified as the type species of the genus. I will petition the International Commission of Zoological Nomenclature ICZN under provisions of Art. 79A accordingly.

Alvania galapagensis Bartsch, 1911, is tentatively placed in *Lirobarleeia* based on external shell characters. No live-collected specimens have ever been found of this deep-water species, so anatomical studies cannot confirm its placement. *Alvania halia* has external sculpture similar to that of *L. nigrescens*, but it is smaller, white, has deeper sutures, and has a distinctly different protoconch.

ACKNOWLEDGMENTS

I am indebted to Kirstie L. Kaiser for collecting the newly cited material of *Lirobarleeia nigrescens* and *Alvania halia* and making it available for study, to M. G. Harasewych, Alan R. Kabat, and Raye N. Germon of the National

Museum of Natural History, Smithsonian Institution, for loan of the types of *Alvania galapagensis*, *Alvania halia*, and *Alvania nigrescens*, and to Winston F. Ponder of the Australian Museum, Sydney (AMS), for loan of two lots of *Lirobarleeia galapagensis* of Ponder, 1983. The late C. Clifton Coney of the Los Angeles County Museum of Natural History (LACM) took the SEM photographs, and David K. Mulliner is thanked for additional photography work. I am most indebted to James H. McLean (LACM) and Winston F. Ponder (AMS) for their continued encouragement and for reading the manuscript. I thank the San Diego Natural History Museum, Marine Invertebrate Department for use of its library and facilities. Figures 2 and 3 are reprinted from Ponder, 1983:264, with permission of the Australian Museum, Sydney.

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NOTES, INFORMATION & NEWS

THANKS, DAVE . . .

For more than a decade, Dr. David W. Phillips served as Editor-in-Chief of *The Veliger*, maintaining the standards of excellence instituted by the journal's founder, Dr. Rudolf Stohler. With finesse and unflagging good humor, Dave juggled the countless tasks involved in producing a quarterly publication, employing his outstanding management and editorial skills to assist *Veliger* contributors—from graduate students crafting a first publication to established professionals—in steering their writings through the review and revision process to reach the ultimate goal of publication in *The Veliger*. This issue as well, featuring the papers of the 1991 bivalve symposium at Moss Landing Marine Laboratories, represents the efforts of Dave Phillips; he guided the manuscripts featured in this issue through review and revision.

On Dave's watch, two of the most significant currents in modern malacology—the discovery and description of a diverse molluscan fauna associated with deep sea hot vents, and the rise of cladistic analysis to reckon the phylogenetic relationships among taxa—have found their expression on the pages of *The Veliger*. Malacology at every level, from the faunistic through the organismal to the molecular, has come to be represented in a journal second in scope to none in its field.

It is characteristic of Dave that, when early in 1993 he decided it was time to move on, he also took steps to ensure that the transfer of editorial responsibility would be smooth and uneventful. He has selflessly helped your new editor ease into the job; any undotted i's or uncrossed t's from now on are my responsibility.

On behalf of the California Malacozoological Society and malacologists everywhere: thanks, Dave . . . for keeping our science and our syntax straight.

Barry Roth

Field Observations of *Rossia pacifica* (Berry, 1911) Egg Masses

by

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Most observations of *Rossia pacifica* reproductive behavior have been made in the laboratory or in public aquaria.

Reproduction and oviposition have been observed in the laboratory (Brocco, 1971; Summers & Colvin, 1989) and in public aquaria (Anderson, 1987a, 1991). In the laboratory, the eggs have commonly been attached to walls of aquaria, bricks, empty shells, and PVC pipe (Summers & Colvin, 1989).

Observations of other aspects of behavior are also sparse. Brocco (1971), Summers (1985), and Summers & Colvin (1989) made behavioral observations in the laboratory. Few *in situ* natural history observations of *R. pacifica* have been reported. Shimek (1983) discussed escape responses and predator avoidance behavior, and Anderson (1987a, b) and Anderson & Vanderwerff (1989) hypothesized annual depth migrations based on their observations made during collection dives for a public aquarium.

No previous observations of *R. pacifica* oviposition and egg capsules in nature have been reported.

We have observed four *R. pacifica* egg clutches during scuba dives and report one other, in different locations in the greater Puget Sound region (Washington State, USA):

18 February 1977, at a depth of 18 m on the outside of a coffee mug, at the base of a cliff under overhanging rocks in Friday Harbor Bay, San Juan Island;

12 February 1991, at a depth of 25 m on the underside of a rock near Hoodspout, Hood Canal; photographed 23 February 1991 (Figure 1);

27 November 1991, at a depth of 25 m on the underside of a rock in Elliott Bay, Seattle;

22 June 1992, at a depth of 30 m on a rock cliff, Pt. Disney, Waldron Island;

14 April 1993, at a depth of 25 m on a flat rock under a rock overhang, WaWa Point, Hood Canal (Jeff Christiansen, Seattle Aquarium, personal communication).

The distinctive egg masses were composed of clusters of white eggs, approximately one cm in diameter. The eggs were sub-spherical or ovoid with a flattened surface cemented to the substrate and a small papilla on the side opposite the attachment.

Four commonalities were apparent in these egg sightings. First, all egg capsules were located in relatively calm waters in areas with little tidal flow. Second, they were all attached to smooth, hard surfaces. Third, all were protected from overhead siltation, generally by overhanging rocks. Fourth, all were in depths greater than 15 m.

The egg clutch in Elliott Bay, Seattle's harbor, was seen during oviposition during a night dive. Numerous *R. pacifica* have been seen in this area, a popular dive site (Anderson, 1987b). The large female laying the eggs had a mantle length approximately 45 mm. She was oriented



Figure 1

Rossia pacifica egg clutch, first seen near Hoodspoint (Washington State) on 12 February 1991 and photographed 23 February 1991. The capsules are in a crevice under a rock. Each capsule is about one cm in diameter.

head upward under the rock overhang, with the eggs she had already laid in front of her. She had deposited approximately 25 eggs; clutch sizes are commonly 50–75 eggs (Summers & Colvin, 1989). The bright divers' lights did not seem to bother her as she stayed with the clutch and did not move.

The eggs were laid with no discernable pattern in an area approximately 8 cm in diameter. Some eggs were abutting one another, others were not touching another egg, and some were laid atop other eggs up to three layers thick. Similar patterns of egg deposition were seen in clutches laid by *R. pacifica* in aquaria (Summers & Colvin, 1989) and for *R. macrosoma* (delle Chiaje, 1829) (Boletzky & Boletzky, 1973).

Other sepiolids lay similar eggs and egg clutches on different substrates. *Sepietta oweniana* (d'Orbigny, 1839) deposits eggs on ascidians and seaweed (Bergstrom & Summers, 1983) and *Euprymna scolopes* Berry, 1913, on dead coral (Singley, 1983). *Euprymna* incorporate sand and rubble into their egg capsules.

We had no indication of egg stage, other than the clutch that we observed being laid, since the eggs were not collected. Although *R. pacifica* eggs may take 4½ to 9 months to hatch and may accumulate diatoms and sediment in the laboratory (Summers & Colvin, 1989), the clutches we

observed had no observable growth on them; this may be because they were laid under overhangs that prevented debris from settling on them.

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**The Diet of *Pisania tinctoria*
(Gastropoda: Buccinidae) in Eastern Florida**

by

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Introduction

Pisania tinctoria (Conrad, 1846) is a small (to 35 mm) buccinid occurring intertidally throughout the western Atlantic from the southeastern United States to Brazil. During a recent visit to the Smithsonian Marine Station at Link Port (Fort Pierce, Florida), we had the opportunity to collect these mollusks and to study their diet.

Materials and Methods

Snails were collected at low tide in April 1991, on boulders composing an artificial embankment on the northern shore of Sebastian Inlet, Brevard County, Florida. The animals were frozen at -80°C within an hour of collection to prevent defecation and later transferred to 70% ethanol. Several specimens were fixed without freezing for dissections and histological examination.

Shells of 40 individuals (12.8–32.0 mm in length, mean \pm 25.6 mm) were dissolved in 8% nitric acid, their stomachs dissected, and stomach contents mounted in glycerin on individual glass slides. Proboscides of two specimens were embedded in paraffin, sectioned, and stained with Masson's triple stain. Two specimens were dissected for studies of gross anatomy.

Results and Discussion

Of the 40 individuals examined for stomach contents, 27 (67.5%) were females. Seven stomachs were empty, all

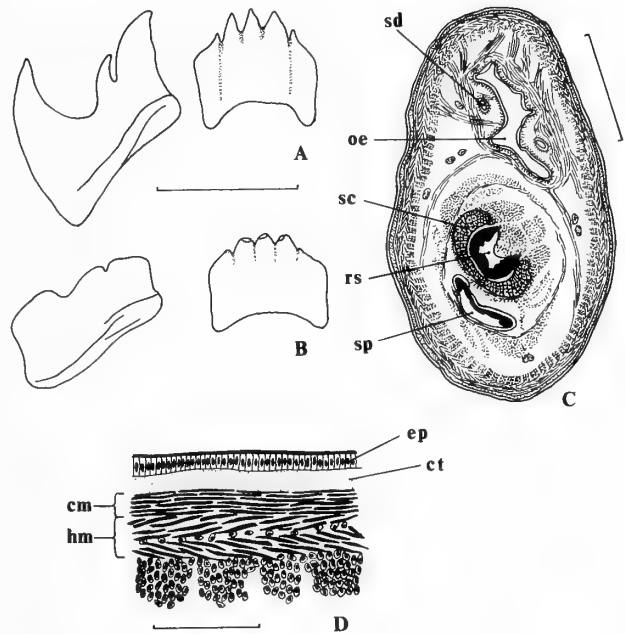


Figure 1

A, B. Half of the radular row of *P. tinctoria* (A. from the central part of the ribbon; B. from the anterior, rasping part of the ribbon); C. Transverse section through the anterior part of the proboscis; D. Enlargement of the transverse section through the proboscis wall.

Scale bars: A, B-0.25 mm; C-0.5 mm; D-0.1 mm.

Abbreviations: cm, circular muscle layer; ct, connective tissue layer; ep, epithelium; hm, helical muscle layer; lm, longitudinal muscle layer; oe, oesophagus; rs, radular sac; sc, subradular cartilages; sd, salivary duct; sp, sublingual pouch.

others contained remnants of the barnacles *Tetraclita stactifera* (Lamarck, 1818) and *Chthamalus fragilis* Darwin, 1854. Most of the stomachs contained tissues of the mantle cavity lining as well as ovaries with eggs. Limbs were found only in three cases. Sand grains and fragments of barnacle shell were also usually present. Barnacles constituted the only recognizable prey item of *P. tinctoria* at this locality.

The anterior (functional) portions of the radulae of all specimens examined were extremely worn (Figure 1B), with the anteriormost 5–11 rows of teeth showing greatest signs of wear. Although we did not observe feeding, the extreme radular wear as well as the presence of barnacle shell fragments in the stomach suggests that the radula is employed in the mechanical penetration of the barnacle's shell.

The gross anatomy of the anterior alimentary system of *P. tinctoria* conforms to the typical buccinid pattern (Ponder, 1973), consisting of a long pleurembolic proboscis, paired acinous salivary glands, a medium-sized long gland of Leiblein, and a poorly differentiated valve of Leiblein.

Table 1

Comparative data on the diet of *Pisania tincta* in different regions of Florida.

Prey	Frequency in diet – % of total prey	
	Pigeon Key*	Sebastian Inlet
<i>Spiroglyphus annulatus</i>	83.9	0
<i>Isognomon bicolor</i> and <i>I. radiatus</i>	8.1	0
Barnacles (<i>Tetraclita stalactifera</i> and <i>Chthamalus fragilis</i>)	0	100
Other	8.0	0
Total observations	263	40

* Data from Ingham & Zischke, 1977.

The structure of the proboscis wall differs from that reported for other Buccinidae studied to date (Medinskaya, 1992). In *Neptunea* and *Buccinum*, the proboscis wall consists of layers of circular and longitudinal muscles interspersed with connective tissue layers, but lacks a helical muscle layer. The proboscis wall of *P. tincta* consists of an outer layer of connective tissue, as well as moderately thick layers of circular, helical and longitudinal muscles (Figure 1D). The presence of a helical muscle layer greatly increases the mobility of the proboscis, as its contraction causes bending and/or torsion of the proboscis along its long axis. The proboscis wall of *P. tincta* is thus more similar to that of *Tritia fratercula* (Dunker, 1860) (Nassariidae) from the Sea of Japan (Medinskaya, 1992). *Tritia fratercula* occupies a similar habitat (rocky intertidal zone) and has a similar diet (Crustacea). The musculature of the proboscis wall thus appears to reflect similarities in diet and feeding mechanism rather than phylogenetic relationships.

The diets of tropical representatives of Buccinidae are relatively poorly known. The few species studied to date appear to be generalists, feeding on polychaetes (e.g., *Engina mendicaria*, *E. alveolata*, *E. zonalis*), gastropods (e.g., *Pisania striata*), or both types of prey (e.g., *Buccinulum corneum*, *Cantharus dorbignyana*, *C. undosus*, *C. fumosus*, *Engina bicolor*) (Taylor, 1987).

The present study on the diet of *P. tincta* reveals this species to be a specialist at this site. Surprisingly, the diet of this species differs dramatically at different localities (Table 1). Ingham & Zischke (1977) reported that, in the Florida Keys, *P. tincta* fed primarily upon the vermetid gastropod *Spiroglyphus annulatus* (Daudin, 1800), while barnacles, which were rare (0.2% relative abundance), were not consumed at all. In our study area, where vermetids were absent, barnacles comprised the only recognized food item. This suggests that *P. tincta* is a specialized predator of sessile organisms with hard exoskeletons. The local availability of suitable prey, however, appears to

determine the diets of individual populations, which may vary greatly even between nearby localities.

This is contribution number 336 of the Smithsonian Marine Station at Link Port.

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Does Copulation Induce Female Maturation in Squid *Todarodes pacificus* (Cephalopoda: Ommastrephidae)?

by

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Environmental factors such as light, temperature, nutrition, or food availability are generally thought to be involved in the ovarian maturation of cephalopods by stimulating the hormonal system (Mangold, 1987). In the Japanese common squid, *Todarodes pacificus*, males mature earlier than females by about a month (Adachi, 1982; Ikeda et al., 1993). Female squid receive spermatophores that contain numerous spermatozoa from males during copulation and then store spermatozoa in the seminal receptacle of the outer lip until spawning (Hamabe, 1962). Based on observations in captivity, female *T. pacificus* begin yolk formation after the first copulation (Ikeda et al., 1993). Moreover, it was confirmed that in natural populations of this species, the advancement of female maturity coincides with the proportion of copulated females (Shimizu & Hamabe, 1966). From these observations, Ikeda et al. (1993) considered that copulation is required for the outset of female yolk formation in *T. pacificus*. In this report, we investigate whether copulation is indeed required.

Immature *T. pacificus* were caught in coastal waters off southern Hokkaido and transported to Usujiri Fisheries Laboratory. The details of collecting and maintenance of *T. pacificus* are described elsewhere (Ikeda et al., 1993; Sakurai et al., 1993). Under cold anesthesia (Sakurai et al., 1993), sex was determined for the squids by observing whether the fourth right arm was hectocotylized as is char-

acteristic for males (Hamabe, 1962). The absence of spermatozoa in the seminal receptacle of the outer lip indicated that females had not copulated. Ten females were placed in a circular tank with running seawater to isolate them from males for several days to determine if yolk formation and ovulation occur without copulation. At the same time, a total of 70 immature *T. pacificus* were placed in a raceway tank system as controls for the maturation process. The ovaries of dead squid in both systems were fixed in Bouin's solution, and the condition of maturity was determined according to the histological maturity scale proposed by Ikeda et al. (1991).

Of the 10 individuals placed in the circular tank, one died 20 days after the onset of the experiment and was found to be a male. However, the squid was immature with few spermatophores in the accessory gland. Nine other squids in the circular tank and four squids in the raceway tank whose captive durations were comparable to those in the circular tank were investigated. Based on histological observation of ovaries of squids in the circular tank, two uncopulated females with captive durations of one day and 11 days were immature, two uncopulated females with a captive duration of 20 days were in the yolk formation stage, and five uncopulated females with a captive duration of over 30 days had ovulated ovum into the oviducts. Histological observations showed that oogenesis occurred normally in experimental females compared with controls in the raceway tank. Moreover, the rate at which yolk formation and ovulation occurred in uncopulated females in the experimental tank was almost identical to that of the copulated females in the control tank, i.e., one copulated female with a captive duration of 25 days was in the yolk formation stage, and three copulated females with a captive duration of over 30 days had ovulated ovum into the oviducts. From these observations, we conclude that contrary to our expectations, copulation does not induce or accelerate female maturation in *T. pacificus*.

A possible relationship exists between copulation and the outset of migration in *T. pacificus* (Nakata, 1984) and in *Illex argentinus* (Rodhouse & Hatfield, 1990) or inducement of spawning in *Illex illecebrosus* (Durward et al., 1980). These possible functions for copulation in *T. pacificus* remain to be determined by future investigations.

Acknowledgments

We acknowledge the staff of Usujiri Fisheries Laboratory and Mr. Y. Hayakawa for their cooperation in rearing squid and Dr. Y. Sakurai for his valuable comments. This research was done as a partial fulfillment of the Ph.D. of Y. Ikeda at Hokkaido University. Contribution number 269 of the Research Institute of North Pacific Fisheries.

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Calcium Content of Planorbid Snails Maintained in Artificial Spring Water on Leaf Lettuce with and without Chalk

by

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Introduction

In discussing methods for rearing freshwater gastropods in the laboratory, several authors have suggested adding chalk to the aquarium to serve as a source of calcium

(MacInnis, 1970; Ulmer, 1970), and this has become standard practice. As mentioned in the above references, the water source for the snails is usually spring, pond, or creek water or an artificial spring water (see Ulmer, 1970, for the formula of a widely used artificial spring water). Snails are usually fed lettuce (MacInnis, 1970) or a more complex diet such as the "milk bone" commercially available for dogs (Ulmer, 1970). In our laboratory, snails are usually maintained on a mixed leaf lettuce-Tetramin® (fish food) diet in artificial spring water with added chalk (Fried & Sherma, 1990).

Although there are numerous studies on calcium uptake in freshwater snails (see Greenaway, 1971 and Thomas et al., 1974 as representative examples), none is concerned specifically with the addition of chalk to the aquarium as a calcium supplement for the snails. The purpose of this study was to determine if chalk added to aquaria containing *Helisoma trivolvis* (Say, 1816) (Colorado strain) and *Biomphalaria glabrata* (Say, 1818) snails maintained in artificial spring water on a leaf lettuce diet increased the calcium content of the snail's shell, body, or hemolymph. Comparisons in calcium content were made with snails maintained under identical conditions but without chalk. The calcium content of lettuce used for snail feeding was also determined. Methods were developed for these analyses based on atomic absorption spectrometry (AAS).

Materials and Methods

Aliquots of stock solutions containing 0.0500 g calcium (Ca)/L and 10.0 g strontium (Sr)/L in 1.0 M hydrochloric acid (HCl) were diluted with 1.0 M HCl to prepare AAS standards having Ca concentrations of 0.500, 1.00, 2.00, 4.00, 8.00, and 14.0 µg/ml and a constant 500 µg/ml concentration of Sr.

Prior to experiments, snails were maintained in aquaria containing about 5 L of artificial spring water and fed *ad libitum* on a mixed diet of leaf lettuce-Tetramin. The aquaria contained added chalk.

Hemolymph, body, and shell samples were obtained from seven-snail pools of *Helisoma trivolvis* maintained with and without chalk for four days and *Biomphalaria glabrata* maintained for 18 days. Hemolymph was refrigerated at 4°C until used, usually within two days after collection from snails, and bodies and shells were dried in a 110°C oven overnight. Hemolymph samples (150–400 µl) measured with a 100 µl Drummond (Broomall, PA) digital microdispenser and weighed body (0.05–0.22 g), shell (0.14–0.58 g), and lettuce (0.10–0.33 g) samples were immersed in a beaker containing 10 ml of concentrated nitric acid for 10 min. The solution was then gently boiled just to dryness on a hot plate, and the residue was dissolved in 20 ml of warm 1.0 M HCl. The solution was quantitatively transferred to a 100 ml volumetric flask, 5 ml of Sr stock solution was added, and the flask was filled to the line with 1.0 M HCl. Prior to AAS analysis, aliquots of snail body solutions from the 100 ml flasks were diluted 1:100 and shell solutions 1:1000 with 1.0 M HCl con-

Table 1

AAS determination of calcium in hemolymph, bodies, and shells of snails maintained with and without chalk.

Snail type (days maintained)	Calcium concentration		
	Hemo- lymph (mmole/L)	Bodies (mg/g)	Shells (mg/g)
With chalk			
<i>Helisoma trivolvis</i> (4)	6.91	150	519
<i>Biomphalaria glabrata</i> (18)	1.67	190	444
Without chalk			
<i>Helisoma trivolvis</i> (4)	8.10	165	551
<i>Biomphalaria glabrata</i> (18)	1.67	254	547

taining 500 µg/ml Sr to produce solutions whose absorbance readings were bracketed within the standard curve.

Solutions were analyzed for calcium content using a Varian SpectraAA-10 computer-controlled atomic absorption spectrometer operated with the following parameters: calcium hollow cathode lamp, 422.7 nm; slit, 0.5 nm; stoichiometric flame: air-11 L/min, acetylene-2.2 L/min; sample flow rate, 6 ml/min; three integrations per absorbance reading, 10 sec each. The ppm readings for the aspirated sample solutions were converted by calculation to mmole/L for hemolymph and mg/g for bodies, shells, and lettuce.

Results and Discussion

Absorbance was found to be linearly related to concentration up to 14 ppm, which was the level of the highest standard employed. Strontium was added in constant amount to each sample and standard to function as a releasing agent, which reacts preferentially with potential interfering anions such as phosphate and reduces their interaction with calcium.

Snails are fed boiled and refrigerated lettuce leaves from which stems are not removed, and they readily eat both the leaf and stem portions. Six typical samples of the lettuce were analyzed and found to have an average calcium concentration of 4.70 mg/g with a range of 2.54–6.41 mg/g. Samples that contained all or mostly leaf tended to have a higher calcium content, while samples with a higher proportion of stem assayed at a lower level.

The calcium concentrations of snail hemolymph, body, and shell samples are shown in Table 1. These data, which are the first such baseline values that have been published for *Biomphalaria* and *Helisoma* snails, show that calcium concentrations in *Helisoma* were much higher than those in respective samples from *Biomphalaria glabrata* and that the presence of chalk did not increase calcium concentrations. The latter finding was not surprising because the artificial spring water used was prepared, according to Ulmer (1970), to contain 11.0 mg of anhydrous calcium chloride per ml of distilled water, and the lettuce was also

a significant source of calcium as documented above. In addition, chalk (calcium carbonate) is practically insoluble in water and probably even less soluble in the artificial water containing calcium chloride. The snails were able to feed directly on the chalk, but the data in Table 1 show that there was no resultant increase in their calcium content due to any feeding on the chalk that may have occurred.

Hemolymph calcium values for 14 species of freshwater and terrestrial mollusks were compiled by Schoffeniels and Gilles (1972). The values ranged from a low of 1.5 mmole/L in the freshwater gastropod *Lymnaea stagnalis* to a high of 12.3 mmole/L in the terrestrial gastropod *Strophocheilus oblongus*. Our hemolymph calcium concentrations, as determined by AAS, are within this range of values that were obtained by use of unspecified analytical methods.

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Literature cited

References in the text should be given by the name of the author(s) followed by the date of publication: for one author (Phillips, 1981), for two authors (Phillips & Smith, 1982), and for more than two (Phillips et al., 1983). The reference need not be cited when author and date are given only as authority for a taxonomic name.

The "literature cited" section should include all (and only) references cited in the text, listed in alphabetical order by author. Each citation must be complete, with all journal titles *unabbreviated*, and in the following forms:

a) Periodicals:

Hickman, C. S. 1992. Reproduction and development of trochacean gastropods. *The Veliger* 35:245-272.

b) Books:

Bequaert, J. C. & W. B. Miller. 1973. *The Mollusks of the Arid Southwest*. University of Arizona Press: Tucson. xvi + 271 pp.

c) Composite works:

Feder, H. M. 1980. Asteroidea: the sea stars. Pp. 117-135 in R. H. Morris, D. P. Abbott & E. C. Haderlie (eds.), *Intertidal Invertebrates of California*. Stanford University Press: Stanford, Calif.

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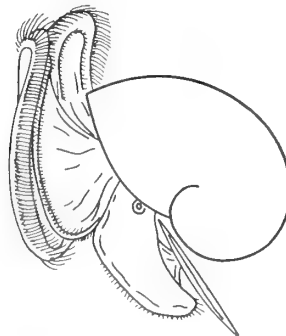
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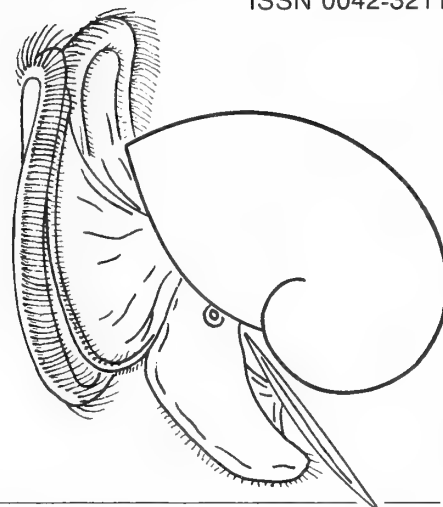


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ISSN 0042-3211

THE VELIGER

A Quarterly published by
CALIFORNIA MALACOOZOOLOGICAL SOCIETY, INC.
Berkeley, California
R. Stohler, Founding Editor

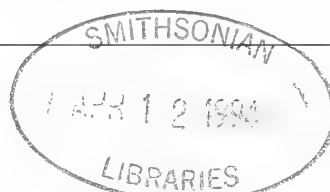


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April 1, 1994

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The Veliger (ISSN 0042-3211) is published quarterly on the first day of January, April, July, and October. Rates for Volume 37 are \$32.00 for affiliate members (including domestic mailing charges) and \$60.00 for libraries and nonmembers (including domestic mailing charges). For subscriptions sent to Canada and Mexico, add US \$4.00; for subscriptions sent to addresses outside of North America, add US \$8.00, which includes air-expedited delivery. Further membership and subscription information appears on the inside cover. The Veliger is published by the California Malacozoological Society, Inc., % Santa Barbara Museum of Natural History, 2559 Puesta del Sol Road, Santa Barbara, CA 93105. Second Class postage paid at Berkeley, CA and additional mailing offices. POSTMASTER: Send address changes to The Veliger, Santa Barbara Museum of Natural History, 2559 Puesta del Sol Road, Santa Barbara, CA 93105.

THE VELIGER

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The Veliger is an international, peer-reviewed scientific quarterly published by the California Malacozoological Society, a non-profit educational organization. *The Veliger* is open to original papers pertaining to any problem connected with mollusks. Manuscripts are considered on the understanding that their contents have not appeared, or will not appear, elsewhere in substantially the same or abbreviated form. Holotypes of new species must be deposited in a recognized public museum, with catalogue numbers provided. Even for non-taxonomic papers, placement of voucher specimens in a museum is strongly encouraged and may be required.

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New Reports of Eocene Mollusks from the Bateque Formation, Baja California Sur, Mexico

by

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Abstract. Seven gastropods and one bivalve are reported for the first time from the Bateque Formation along the Pacific coast of Baja California Sur, Mexico. They are shallow-marine, warm-water mollusks found in scattered lenses of short-distance storm accumulations. Four of the gastropods are from the "Capay Stage" (middle lower Eocene) part of the formation: *Diodora batequensis*; *Gisortia* cf. *G. clarki* Ingram, 1940; *Galeodea* (*Caliagaleodea*) *californica* Clark, 1942; and *Phalium* (*Semicassis*) *louella* Squires & Advocate, 1986. *Diodora batequensis* is the earliest identifiable species of this genus from the Pacific coast of North America. *Gisortia* (*Megalocypraea*) cf. *G. (M.) clarki* and *Phalium* (*Semicassis*) *louella* were previously known from "Capay Stage" strata in southern California and *Galeodea* (*Caliagaleodea*) *californica* was previously known only from the "Domengine Stage" (upper lower Eocene to lower middle Eocene) strata in southern California.

The other three gastropods are from the "Domengine Stage" part of the Bateque Formation: *Dirocerithium* sp., *Cirsotrema eocenica*, and *Architectonica* (*A.*) *llajasensis* Sutherland, 1966. *Dirocerithium* was previously known only from the southeastern United States and the Caribbean region. *Cirsotrema eocenica*, which is also present in southern California, is the earliest species of this genus from the Pacific coast of North America. *Architectonica* (*A.*) *llajasensis* was previously known only from southern California.

The bivalve, *Pycnodonte* (*Phygraea*) *cuarentaensis* is from the "Capay Stage" and is one of the earliest species of this subgenus on the Pacific coast of North America.

INTRODUCTION

Squires & Demetrion (1992) did a monographic-style study of the macro-sized invertebrate fossils of the middle lower Eocene ("Capay Stage") to upper middle Eocene ("Tejon Stage") Bateque Formation, Baja California Sur, Mexico. The formation crops out along the Pacific coast from the eastern Laguna San Ignacio area to the San Juanico area about 105 km to the south (Figure 1). We reported 99 species of macrofossils that included algae, large benthic foraminifers, sponges, hydrozoans, octocorals, gorgonians, colonial and solitary corals, bryozoans, polychaete worms, scaphopods, numerous gastropods and bivalves, nautiloids,

crabs, and echinoids. The macrofossil fauna is indicative of shallow, warm-water conditions. Most of the macrofossils underwent a short distance of postmortem transport and accumulated as channel-lag deposits closely adjacent to coral reef(?) -inhabited shoal areas.

In 1992 and 1993, we returned to the field and resampled some exposures of the Bateque Formation and visited additional exposures in the central part of the outcrop area that were previously inaccessible due to extensive rain-filled playas or extensive sand drifts. We found seven gastropods and one bivalve that were not previously known from the Bateque Formation. They were found in channel-lag storm-bed accumulations, but their shells show little



Figure 1

Index map to CSUN collecting localities, Bateque Formation, Baja California Sur, Mexico. (After Squires & Demetron, 1990: fig. 1).

evidence of abrasion, an indication of short-distance post-mortem transport. Four of the gastropods (*Diodora batequensis*, *Gisortia* (*Megalocypraea*) cf. *G. (M.) clarki* Ingram, 1940, *Galeodea* (*Caliagaleodea*) *californica* Clark, 1942, and *Phalium* (*Semicassis*) *louella* Squires & Advocate, 1986) and the bivalve *Pycnodonte* (*Phygraea*) *cuarentaensis* were determined to be from the "Capay Stage" (middle lower Eocene) part of the Bateque Formation based on their co-occurrence with the following age-diagnostic mollusks: the gastropod *Velates perversus* (Gmelin, 1791) and the bivalve *Spondylus batequensis* Squires & Demetron, 1990. Both species are known only with certainty from this stage in the Bateque Formation and elsewhere on the Pacific coast of North America (Squires & Demetron, 1992). The other three gastropods (*Dirocerithium* sp., *Cirsotrema eocenica*, and *Architectonica (A.) llajasensis* Sutherland, 1966) were determined to be from the "Domengine Stage" (upper lower Eocene to lower middle Eocene) part of the Bateque Formation based on their co-occurrence with the age-diagnostic gastropod *Turritella andersoni lawsoni* Dickerson, 1916. This turritellid is known from this stage in the Bateque Formation and elsewhere on the

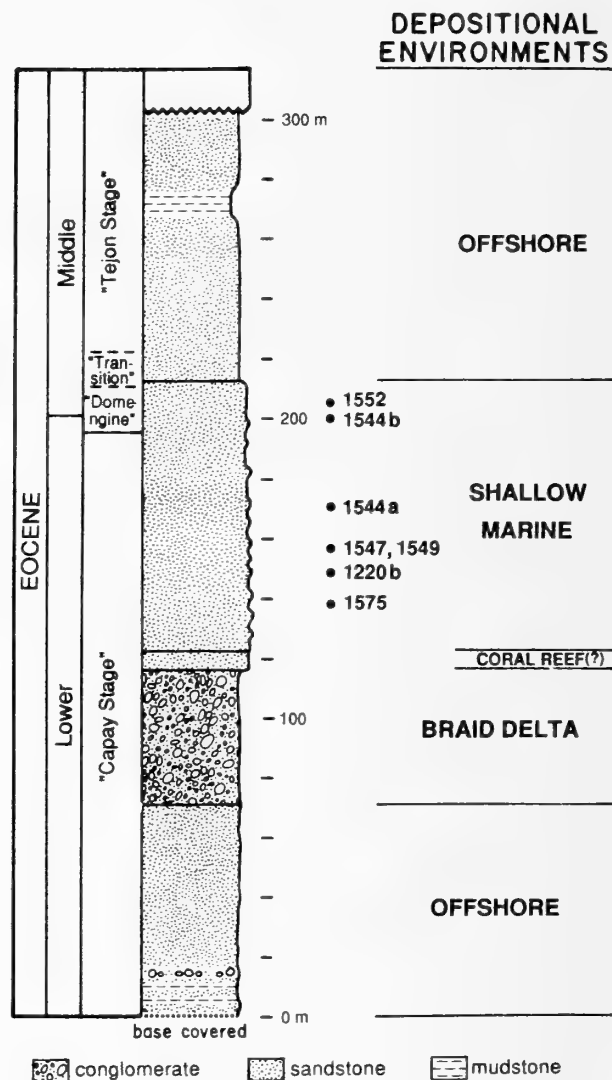


Figure 2

Columnar section of the Bateque Formation showing Pacific coast of North America provincial molluscan stages, stratigraphic position of CSUN macrofossil localities, and deposition environments. (After Squires & Demetron, 1992:fig. 2).

Pacific coast of North America (Squires & Demetron, 1992) (Figure 2).

The new species of *Diodora*, *Cirsotrema*, and *Pycnodonte* (*Phygraea*) have close affinity with Old World Tethyan species and provide evidence in addition to that discussed in Squires (1987) for a paleo-oceanographic connection between the Old World and the Pacific coast of North America. All of the previously named species are known from southern California, and *Gisortia* (*Megalocypraea*) *clarki* and *Phalium* (*Semicassis*) *louella* have also been reported (Clark & Vokes, 1936; Squires & Advocate, 1986) as having close affinity with Old World Tethyan species. *Dirocerithium*, known previously only from the southeast-

ern United States and the Caribbean region, also presumably had a Tethyan ancestry (Woodring, 1959).

The molluscan stages used in this report stem from Clark & Vokes (1936), who proposed five mollusk-based provincial Eocene stages, namely, "Meganos," "Capay," "Domengine," "Transition," and "Tejon." The stage names are in quotes because they are informal terms. Givens (1974) modified the use of the "Capay Stage," and it is in this modified sense that the "Capay Stage" is used herein.

The classification system used for gastropod taxonomic categories higher than the family level generally follows that of Ponder & Warén (1988). The classification scheme used for pycnodontid oysters follows that of Stenzel (1971).

Abbreviations used for catalog and/or locality numbers are: CSUN, California State University, Northridge; IGM, Instituto de Geología, Universidad Nacional Autónoma de México; LACMIP, Natural History Museum of Los Angeles County, Invertebrate Paleontology Section; UCMP, University of California Museum of Paleontology (Berkeley).

SYSTEMATIC PALEONTOLOGY

Class Gastropoda Cuvier, 1797

Order Vetigastropoda Salvini-Plawén, 1980

Family FISSURELLIDAE Fleming, 1822

Genus *Diodora* Gray, 1821

Type species: *Patella apertura* Montagu, 1803 [= *Patella graeca* Linné, 1758], by original designation, Recent, British Isles.

Diodora batequensis Squires & Demetrion, sp. nov.

(Figures 3–6)

Diagnosis: A *Diodora* with a very small perforation that narrows posteriorly, a partially intact apex, and 14 primary radial ribs.

Description: Shell small, thin, low conical with height about 40 percent of the length, base flat, aperture oval. Apex partially intact, blunt pointed, situated just in advance of middle of shell. Anterior slope moderately steep, posterior slope angle less than that of anterior slope angle. Perforation very small, just anterior to apex, anterior end of perforation rounded, posterior end narrower. Sculpture consisting of about 14 primary radial ribs originating at apex. Interspaces between primary radial ribs with a single secondary radial rib emerging near apex and becoming stronger at margin. Interspaces between secondary radial ribs with a faint tertiary radial rib. Concentric sculpture consisting of about 16 ribs, giving shell a cancellate appearance. Interior callus low and truncate posteriorly.

Holotype: IGM 5951 (= plastoholotype LACMIP 12251).

Type locality: CSUN loc. 1220b, eastern Laguna San

Ignacio area, Baja California Sur, Mexico, 112°59'40"W and 26°44'40"N.

Dimensions: Holotype, length 10.2 mm, width 8.0 mm, height 4 mm.

Discussion: Only a single specimen of the new species was found. It is a very rare specimen, when one considers that we have spent innumerable hours over the last six years collecting macrofossils from the Bateque Formation. The holotype appears to be a mature specimen (J. H. McLean, personal communication).

The new species most closely resembles *Diodora incerta* (Deshayes, 1866:237, pl. 7, figs. 25–27; Cossmann & Pissarro, 1910–1913:pl. 2, fig. 6–4) from middle Eocene (Lutetian Stage) rocks of the Paris Basin, France. The new species differs in having a much smaller perforation and fewer but more prominent primary radial ribs.

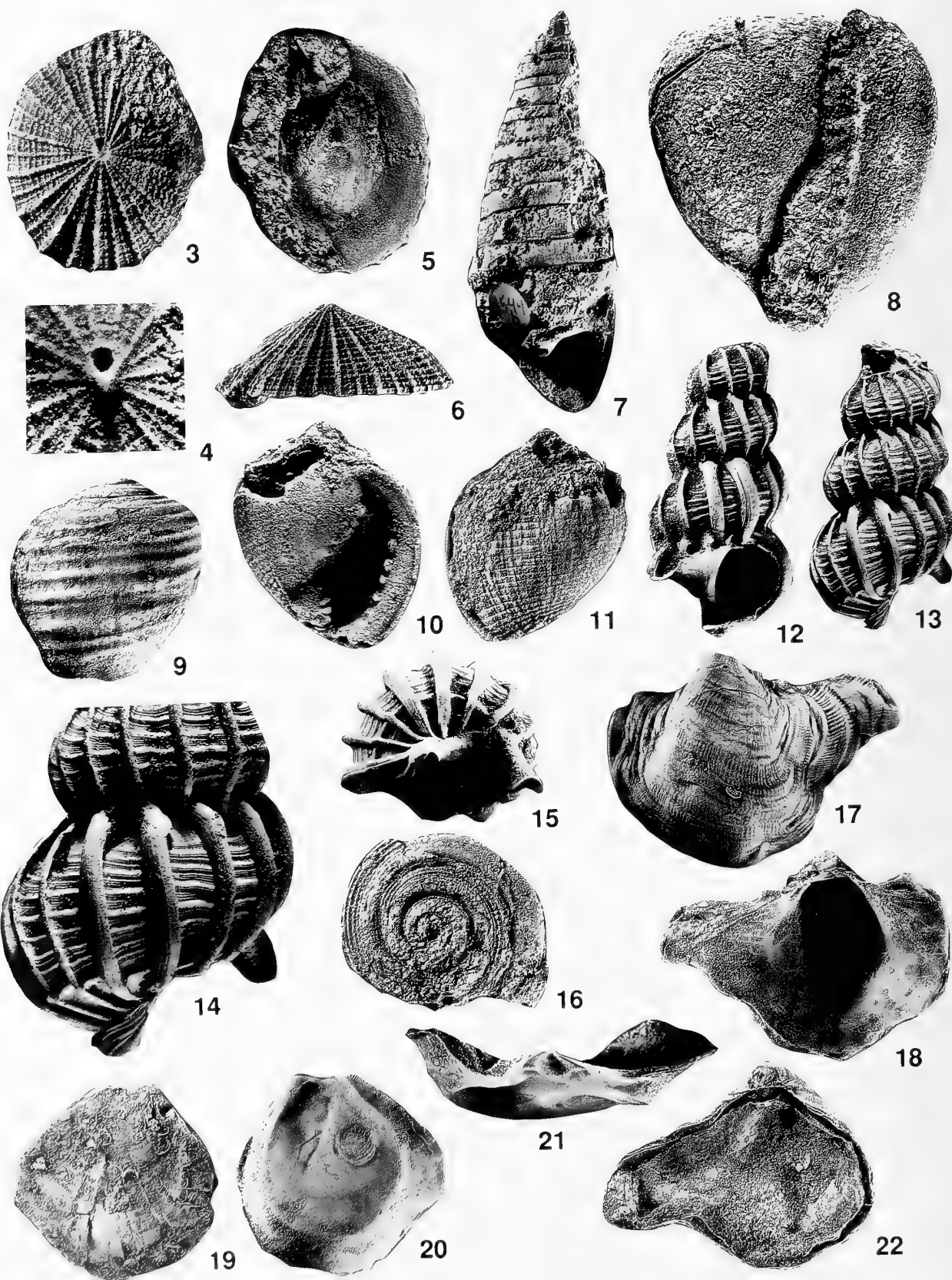
Diodora batequensis has no apparent ancestor among indigenous Paleocene or Late Cretaceous faunas. The only other Eocene *Diodora* known from the Pacific coast of North America is *D. stillwaterensis* (Weaver & Palmer, 1922:27, pl. 11, figs. 3, 6; Weaver, 1942 [1943]:284, pl. 63, fig. 20; pl. 64, figs. 4, 7, 12) from the Cowlitz Formation, Lewis and Cowlitz Counties, southwestern Washington. Armentrout et al. (1983) assigned this formation to a late middle Eocene age. Squires & Deméré (1991: figs. 3A, B) reported that *D. stillwaterensis* may be present in the middle Eocene Frairs Formation, San Diego County, southern California. *Diodora batequensis* differs from *D. stillwaterensis* by having a partially intact apex, a much smaller perforation, 14 rather than 28 primary radial ribs, and much fewer concentric ribs. Squires & Goedert (in review) reported a few specimens of *Diodora* sp. indet. from the "Capay Stage" part of the Crescent Formation, Little River area, western Washington. These specimens are internal molds that show evidence of the truncate internal callus that is diagnostic of genus *Diodora* and show evidence of a reticulate sculpture pattern that closely resembles *D. stillwaterensis*.

Diodora has been reported from Paleocene and Eocene rocks of the eastern and southeastern United States (Palmer & Brann, 1966), but these species differ from the new species by having no apex (or only the slightest hint of one) and by having a large perforation.

Wenz (1938) and Keen (1960) reported the geologic range of genus *Diodora* to be Late Cretaceous to Recent. Sohl (1992) reported that Cretaceous species of so-called *Diodora* are very rare and the generic status of most of these species is open to question. Two of the earliest known species that can be positively assigned to genus *Diodora* are from Upper Cretaceous (Maastrichtian Stage) strata. One species is from Puerto Rico and the other is from Jamaica (Sohl, 1992).

Etymology: The specific name is for the Bateque Formation.

Occurrence: "Capay Stage" (middle lower Eocene). Ba-



teque Formation, eastern Laguna San Ignacio area, Baja California Sur, Mexico, CSUN loc. 1220b.

Order Caenogastropoda Cox, 1960

Family CERITHIIDAE Fleming, 1822

Genus *Dirocerithium* Woodring & Stenzel in
Woodring, 1959

Type species: *Dirocerithium wechesense* Stenzel in Woodring, 1959, by original designation, middle Eocene, Texas.

Dirocerithium sp.

(Figure 7)

Discussion: Three broken specimens of a cerithioid gastropod with very distinctive sculpture were found in "Domengine Stage" (upper lower Eocene to lower middle Eocene) strata at CSUN loc. 1544b. The largest specimen (Figure 7), which is 51 mm in height, has the best preservation and shows a fusiform shape with two wide and flat bands per whorl. These bands are separated by a spiral groove, and the posteriormost band is the widest (at least on the spire whorls). Early whorls are sculptured with numerous axial ribs extending from suture to suture and possessing small nodes immediately anterior to the spiral groove separating the two bands. Axial ribbing is obsolete on the later whorls. The anteriormost band is covered by many minute, nearly microscopic spiral threads.

The Bateque Formation specimens of *Dirocerithium* sp. most likely represent a new species, but this determination cannot be made because of the incompleteness of the specimens. The aperture and uppermost spire whorls are missing, and the upper spire whorls are only partially preserved. The specimens are most similar to both *Dirocerithium ame* Woodring (1959:175–176, pl. 24, figs. 15–18) from the middle Eocene Gatuncillo Formation, Panama Canal Zone, and to what Woodring (1959) identified as *D. cf. D. mariense* (Trechmann, 1924:3, pl. 2, fig. 3)) from the

upper Eocene of Columbia. Clark & Durham (1946:29, pl. 24, fig. 1) had originally identified the Colombian specimens as *Clava* (*Ochetoclava*) aff. *vineta* (Whitfield, 1985).

Dirocerithium is an Eocene genus known only from a few species in southeastern United States, Cuba, Jamaica, Panama Canal Zone, and Colombia. Woodring (1959:174) listed these species and reported that *Dirocerithium* ranges in age from early middle Eocene to late Eocene. The Bateque Formation specimens of *Dirocerithium*, along with *D. mariense* (Trechmann, 1924:13, pl. 2, fig. 3) from Jamaica, are the earliest representatives of this genus. *Dirocerithium* has not been previously reported from the Pacific coast of North America.

Family CYPRAEIDAE Rafinesque, 1815

Genus *Gisortia* Jousseaume, 1884a

Type species: *Ovula gisortiana* Passy, 1859, by subsequent designation (Jousseaume, 1884b), Lutetian Stage (middle Eocene), Gisors, northern France.

Subgenus *Megalocypraea* Schilder, 1927

Type species: *Megalocypraea ovumstruthionis* Schilder, 1927, by original designation, Lutetian Stage (middle Eocene), Bavaria.

Gisortia (*Megalocypraea*)

cf. *G. (M.) clarki* Ingram, 1940

(Figure 8)

Discussion: Only four specimens were found, and they are large-sized internal molds ranging in height from 7.5 to 9.0 cm. Three of the specimens are from CSUN loc. 1544a, and the other specimen is from CSUN loc. 1220b. Although the internal molds do not allow for positive species identification, the specimens possess a high dorsal convexity, a flat venter, and an aperture that curves more to the left posteriorly than it does anteriorly. These features strongly resemble *Gisortia* (*Megalocypraea*) *clarki* Ingram

Explanation of Figures 3 to 22

Figures 3–6. *Diodora batequensis* Squires & Demetrion, sp. nov., holotype IGM 5951 from CSUN loc. 1220b. Figure 3: dorsal view, $\times 4$. Figure 4: close-up of apical area, $\times 12$. Figure 5: interior view, $\times 4$. Figure 6: left-lateral view, $\times 4$. Figure 7. *Dirocerithium* sp., hypotype IGM 5952 from CSUN loc. 1554b, apertural view (aperture missing), $\times 1.33$. Figure 8. *Gisortia* (*Megalocypraea*) cf. *G. (M.) clarki* Ingram, 1940, hypotype IGM 5953 from CSUN loc. 1544a, internal mold, apertural view, $\times 0.76$. Figure 9. *Galeodea* (*Caliagaleodea*) *californica* Clark, 1942, hypotype IGM 6377 from CSUN loc. 1575, internal mold, abapertural view, $\times 1.63$. Figures 10–11. *Phalium* (*Semicassis*) *louella* Squires & Advocate, 1986, hypotype IGM 6378 from CSUN loc. 1220b, $\times 3$. Figure 10: apertural view. Figure 11: abapertural view. Figures 12–15. *Cirsotrema eocenica* Squires & Demetrion, sp. nov., holotype IGM 6379 from CSUN loc. 1552. Figure 12: apertural view, $\times 1.42$. Figure 13: abapertural view, $\times 1.42$. Figure 14: close-up of body whorl, abapertural view, $\times 3$. Figure 15: basal view, $\times 2$. Figure 16. *Architectonica* (*Architectonica*) *llajasensis* Sutherland, 1966, hypotype IGM 6380 from CSUN loc. 1544b, dorsal view, $\times 2.73$. Figures 17–22. *Pycnodonte* (*Phygraea*) *cuarentaensis* Squires & Demetrion, sp. nov. from CSUN loc. 1547. Figures 17–18: holotype IGM 6381. Figure 17: left-valve exterior, $\times 1.22$. Figure 18: left-valve interior, $\times 1.22$. Figures 19–21: paratype IGM 6382. Figure 19: right-valve exterior, $\times 1.55$. Figure 20: right-valve interior, $\times 1.55$. Figure 21: dorsal view, $\times 2.3$. Figure 22: paratype IGM 6383, an articulated specimen showing right-valve exterior, $\times 1.2$.

(1940:376–377, fig. 1; Grooves, 1992:figs. 3a, 3b) known from “Capay Stage” strata of Simi Valley, southern California and southern San Joaquin Valley, south-central California (Squires, 1987).

Genus *Gisortia* is herein reported for the first time from Mexico.

Family CASSIDAE Swainson, 1832

Genus *Galeodea* Link, 1807

Type species: *Buccinum echinophorum* Linné, 1758, by monotypy, Recent, Mediterranean Sea.

Subgenus *Caliagaleodea* Clark, 1942

Type species: *Caliagaleodea californica* Clark, 1942, by original designation, “Domengine Stage” (upper lower to lower middle Eocene), Simi Valley, southern California.

Galeodea (*Caliagaleodea*) *californica* Clark, 1942

(Figure 9)

Galeodea (*Caliagaleodea*) *californica* Clark, 1942:118–119, pl. 19, figs. 15–19. Squires, 1984:26, fig. 7j.

Galeodea californica Clark. Givens & Kennedy, 1979:table 1.

Type material and type locality: Holotype UCMP 34376, paratype UCMP 34377; both from the Lajas Formation, Simi Valley, southern California, UCMP loc. 7004.

Geographic distribution: Northwest of San José de Gracia, Baja California Sur, Mexico to Simi Valley, southern California.

Stratigraphic distribution: “Capay Stage” (middle lower Eocene to “Domengine Stage” (upper lower Eocene to lower middle Eocene); equivalent to Ypresian to Lutetian Stages of Europe. “Capay Stage”: Bateque Formation, northwest of San José de Gracia, Baja California Sur, Mexico (herein). “Domengine Stage”: Scripps Formation, near San Diego, San Diego County, southern California (Givens & Kennedy, 1979); Lajas Formation (informal “Stewart bed”), north side of Simi Valley, Ventura County, southern California (Squires, 1984).

Discussion: Only two specimens were found in the Bateque Formation. Both are fairly complete, with the largest one 34 mm in height, and they are both from CSUN loc. 1575. They are internal molds, but they clearly show evidence of the diagnostic sculpture that consisted of prominent spiral ribbing with no axial ribbing. Previously, this species was known only from the “Domengine Stage” in southern California (Squires, 1984). The presence of this species at CSUN loc. 1575 extends its geologic range into the “Capay Stage.”

An unidentified species of *Galeodea* was previously reported (Squires & Demetron, 1992) from the “Capay

Stage” part of the Bateque Formation. These specimens are unlike *G. (C.) californica* in that they have prominent nodes on the body whorl shoulder and do not possess the prominent spiral ribbing on the body whorl.

Genus *Phalium* Link, 1807

Type species: *Buccinum glaucum* Linné, 1758, by subsequent designation (Dall, 1909), Recent, Indo-Pacific.

Subgenus *Semicassis* Mörch, 1852

Type species: *Cassis japonica* Reeve, 1848 [1849], by subsequent designation (Harris, 1897), Recent, Indo-Pacific.

Phalium (*Semicassis*) *louella* Squires & Advocate, 1986

(Figures 10–11)

Phalium (*Semicassis*) *louella* Squires & Advocate, 1986:858–859, figs. 2.11, 2.12.

Type material and type locality: Holotype LACMIP 7166; paratype LACMIP 7177; both from Maniobra Formation, Orocopia Mountains, southern California, CSUN loc. 665.

Geographic distribution: Eastern Laguna San Ignacio area, Baja California Sur, Mexico to Orocopia Mountains, Riverside County, southern California.

Stratigraphic distribution: “Capay Stage” (middle lower Eocene). Bateque Formation, eastern Laguna San Ignacio area, Baja California Sur, Mexico (herein); Maniobra Formation, Orocopia Mountains, Riverside County, southern California (Squires & Advocate, 1986).

Discussion: Only a single specimen was found, and it is a small specimen from CSUN loc. 1220b. The spire is an internal mold, but the body whorl shows the diagnostic closely spaced, fine spiral ribs, numerous small nodes on the shoulder, a less nodose carina on the middle part of the whorl, and a third carina (very faint) near the anterior part of the whorl. The Bateque Formation specimen shows the apertural details that were previously unknown for this species. There is a varix on the outer lip, and the inside edge of the outer lip bears seven teeth (the anteriormost two are the weakest). The anterior part of the inner lip is affected by the siphonal fasciole and bears at least three teeth. The anteriormost part of the aperture is missing. A thin callus with five small denticles in the parietal area spreads roundly over the apertural face of the body whorl. The anterior margin of the callus is raised in the region of the siphonal fasciole.

Family EPITONIIDAE Lamarck, 1822

Genus *Cirsotrema* Mörch, 1852

Type species: *Scalaria varicosa* Lamarck, 1822, by monotypy, Recent, western Pacific Ocean.

Cirsotrema eocenica Squires & Demetron, sp. nov.

(Figures 12–15)

Cirsotrema sp. Squires, 1984:21, fig. 6p.

Diagnosis: A *Cirsotrema* with approximately 12 axial ribs and seven to eight spiral ribs.

Description: Shell medium-sized, moderately thick, turritiform with strongly convex teleoconch whorls and deep sutures. Axial ribs bladelike with tendency to become lamellose on body whorl, bladelike ribs 0.25 to 0.50 mm thick, lamellose ribs 1.25 to 2 mm thick. Axial ribs extending onto base of body whorl with approximately 12 per whorl and arranged in a usually continuous series and fused across the suture. Axial ribs deflected abaperturally near suture and forming triangular-shaped thickenings. Interspaces between bladelike axial ribs approximately five times as wide as ribs. Interspaces between lamellose axial ribs approximately three times as wide as ribs. Primary spiral ribs well-developed, approximately seven to eight per whorl, but obsolete below suture and replaced on base of body whorl by very fine, secondary spiral threads. Interspaces between spiral ribs twice as wide as spiral ribs and showing approximately five very fine spiral ribs. All spiral ribs (primary and secondary) extending onto backs of axial ribs. Basal spiral keel well-developed and originating from posterior section of aperture. Aperture ovate, peristome continuous and thickened, especially on outer lip area. Fasciole narrow.

Holotype: IGM 6379 (= plastoholotype LACMIP 12252).

Type locality: CSUN loc. 1552, San José de Gracia area, Baja California Sur, Mexico, 112°45'15"W and 25°32'40"W.

Dimensions: Holotype, height 35.1 mm [incomplete], width 17.9 mm.

Discussion: Only the holotype and a small fragment of the new species were found at the type locality in the "Domengine Stage" part of the Bateque Formation. Squires & Demetron, (1992:30, fig. 67) reported a broken specimen of an *Epitonium* sp. from CSUN loc. 1220b in the "Capay Stage" part of the Bateque Formation. The new species superficially resembles this "Capay Stage" species, but the new species differs by having 12 rather than 20 axial ribs and by having the ribs more strongly lamellose.

The new species is also present in the "Domengine State" part of the Llajas Formation, Simi Valley, southern California, where Squires (1984) reported a single specimen as an unidentified species of *Cirsotrema*.

The new species resembles *Cirsotrema contabulata* Deshayes (1864–1866:334, pl. 11, figs. 11–12; Cossmann, 1888:134–135, pl. 5, fig. 19; Cossmann & Pissarro, 1910–1913, pl. 7, fig. 52–22) from the Ypresian Stage (lower Eocene) of the Paris Basin, France. The new species differs in the following features: larger size, narrower teleoconch,

fewer spiral ribs and wider interspaces, obsolescence of spiral ribs near sutures, and axial ribs of variable strength.

The new species is the only named Eocene species of genus *Cirsotrema* from the Pacific coast of North America, and is the earliest *Cirsotrema* from this area. Durham (1937:492) reported a poorly preserved, unnamed species of late? Eocene age from Fresno County, central California. The new species differs by having 12 to 13 rather than nine axial ribs. When compared to the five other North American Pacific coast species of post-Eocene *Cirsotrema* reviewed by Durham (1937), the new species is most similar to *C. howei* Durham (1937:492, pl. 56, fig. 8) from the Pliocene of Coos Bay, Oregon. The new species differs by having 12 to 13 rather than nine axial ribs, seven to eight rather than four primary spiral ribs, and much wider interspaces with more secondary spiral ribbing.

The new species also resembles certain specimens of *Cirsotrema togatum* (Hertlein & Strong, 1951) illustrated by DuShane (1988:56, figs. 10–11) from the Pliocene Esmeraldas beds, Ecuador, and from modern shallow waters (32 to 113 m depths) throughout the Gulf of California to Costa Rica and the Galápagos Islands. The new species has more spiral ribs and a much less tabular shoulder on the whorls.

Wenz (1940) reported the geologic range of genus *Cirsotrema* to be Eocene to Recent. *Cirsotrema* probably originated in the Old World Tethyan paleobiota province and immigrated to the Pacific coast of North America during the early part of the Eocene.

The placement of family Epitonidae in the hierarchy of gastropod classification is in a stage of revision. Most recent workers would probably agree with Ponder & Warren (1988:303) and cautiously place the family in the ptenoglossa group of caenogastropods.

Etymology: The specific name is for the Eocene.

Occurrence: "Domengine Stage" (upper lower Eocene to lower middle Eocene). Bateque Formation, San José de Gracia area, Baja California Sur, Mexico (herein); Llajas Formation (informal "Stewart bed" near middle of formation), north side of Simi Valley, Ventura County, southern California (Squires, 1984).

Order Heterostropha Fischer, 1885

Family ARCHITECTONICIDAE Gray, 1850

Genus *Architectonica* Röding, 1798

Type species: *Trochus perspectivus* Linné, 1758, by subsequent designation (Gray, 1847), Recent, Indo-Pacific.

Subgenus *Architectonica* s.s.

Architectonica (*Architectonica*) *llajasensis*
Sutherland, 1966

(Figure 16)

Architectonica llajasensis Sutherland, 1966:1–4, figs. 1–2.
Squires, 1984:19, fig. 6k.

Type material and type locality: Holotype LACMIP 1140, Llajas Formation, Simi Valley, southern California, LACMIP loc. 461-B.

Geographic distribution: Eastern Laguna San Ignacio area, Baja California Sur, Mexico to northern side of Simi Valley, Ventura County, southern California.

Stratigraphic distribution: “Domengine Stage” (upper lower Eocene to lower middle Eocene). Bateque Formation, eastern Laguna San Ignacio area, Baja California Sur, Mexico (herein); Llajas Formation, north side of Simi Valley, Ventura County, southern California (Sutherland, 1966; Squires, 1984).

Discussion: The single specimen found is from CSUN loc. 1544b. The specimen is not too well-preserved, but it shows the eight closely spaced and beaded spiral ribs that are diagnostic of this species. An additional specimen that might be this species was found at CSUN loc. 1552, but poor preservation prevents positive specific identification. Previously, *A. (A.) llajasensis* was known only from the north side of Simi Valley, Ventura County, southern California.

The genus *Architectonica* has been previously reported from the Bateque Formation by Squires & Demetron (1992), who found *A. (Stellaxis) cognata* (Anderson & Hanna, 1925) in the “Capay Stage” part of the formation. *Architectonica (A.) llajasensis* differs from *A. (S.) cognata* by possessing many closely spaced spiral ribs and beaded spiral ribs.

Class Bivalvia Linné, 1758

Order Pterioidea Newell, 1965

Family GRYPHAEIDAE Vyalov, 1936

Genus *Pycnodonte* Fischer de Waldheim, 1835

Type species: *Pycnodonte radiata* Fischer de Waldheim, 1835, by original designation, Upper Cretaceous, Crimea.

Subgenus *Phygraea* Vyalov, 1936

Type species: *Phygraea frauscheri* Vyalov, 1936 [= *Gryphaea pseudovesicularis* Gümbel, 1861], by original designation, upper Paleocene, Austria.

Pycnodonte (Phygraea) cuarentaensis
Squires & Demetron, sp. nov.

(Figures 17–22)

Diagnosis: A medium-sized *Phygraea* with fine radial ribs on left valve and a posterior winglike extension of the shell.

Description: Shell medium-sized, up to 38 mm high and 40 mm long (same specimen), thin, alate, strongly inequivalved. Ligamental pit in both valves small. Left valve very convex, covered with fine radial ribs, umbo subcentral,

in some specimens incurved and used as attachment to substrate. Posterodorsal margin of left valve with prominent winglike extension roughly half the length of the valve and separated from main part of valve by shallow to moderately deep sulcus. Interior of left valve smooth, except for several closely spaced very thin irregular growth lamellae along dorsal area of winglike extension. Right valve concave, rarely somewhat flattened, same shape but slightly smaller than corresponding left valve, exterior usually smooth with some irregular, widely spaced, radial gashes but rarely with very fine radial ribs in umbo area. Margin of right valve deflected upward to accommodate fitting within left valve. Ligamental pit bent backward and exposed along margin of valve. Interior of right valve smooth with or without a few commarginal raised areas corresponding to former position of prominent commissural shelf edge. Minute vermicular anachomata not very extensive and rarely evident. Adductor-muscle scar circular, situated just posterior and dorsal of center of right valve. Deflected-upward margins of right valve smooth with finely granular appearance due to vesicular shell structure.

Holotype: IGM 6381 (= plastoholotype LACMIP 12253).

Type locality: CSUN loc. 1547, northwest of San José de Gracia, Baja California Sur, Mexico. 112°53'13"W and 26°38'50"N.

Paratypes: IGM 6382, 6383 [both from CSUN loc. 1547] (= plastoparatypes LACMIP 12254, 12255).

Dimension: Of holotype, height 31 mm, length 41.7 mm, thickness 17 mm; paratype 6382, height 22.8 mm, length 23.5 mm; paratype 6383, height 30.5 mm, length 39.3 mm.

Discussion: Extremely abundant specimens were found at CSUN loc. 1547 and 1549, where their remains totally dominate the lenticular fossiliferous beds. Preservation is good to excellent. The specimens are mostly disarticulated and are mostly left valves, except at locality 1547 where there are both single left and right valves, as well as some articulated specimens. Some of the specimens served as substrate for juvenile specimens. A few specimens were found at CSUN loc. 1575.

As illustrated in Figure 22, the right valve of the new species is slightly smaller than the corresponding left valve. Hayami & Kase (1992) noted that “size discordance” between valves is a commonly reported feature in species of *Pycnodonte*, and they suggested that the difference may be only superficial because the margin of the right valve was physically weak and was selectively lost before fossilization. Based on their study of the only living species of *Pycnodonte* s.s., they determined that the right valve has a flexible distal area and that the radial gashes on the exterior of the right valve may contribute an increased flexibility to the distal part.

The new species most closely resembles *Ostrea profunda* Deshayes (1824–1837:pl. 48, figs. 4, 5; Cossmann & Pisarro, 1904–1906:pl. 43, fig. 135–5) from the Lutetian

Stage (middle Eocene) of the Paris Basin, France. The new species differs in having radial ribbing on the left valve, a more elongate winglike extension of the posterior part of the shell, and a more distinct sulcus between the winglike extension and the main part of the shell.

Stenzel (1971) reported *Pycnodonte* as ranging from Cretaceous to Miocene and worldwide, but according to Hayami & Kase (1992), the genus ranges from late Early Cretaceous to Recent and is known almost exclusively from low-middle latitudinal regions. A large number of fossil species of *Pycnodonte* (including subgenus *Phygraea*) are known mainly in the Old World Tethyan realms from the late Early Cretaceous to early Miocene (Hayami & Kase, 1992). Additionally, Hayami & Kase (1992) provided an updated review of the systematics of pycnodontid oysters and included a discussion of the subgeneric division of genus *Pycnodonte*.

Pycnodonte (*Phygraea*) *cuarentaensis* sp. nov. is only the second report of the subgenus on the Pacific coast of North America. The other report is *P. (P.) pacifica* (Squires & Demetron (1990:386, fig. 3.1–3.4) from the “Capay Stage” to the middle Eocene part of the “Tejon Stage” strata in the Bateque Formation. The new species differs from *P. (P.) pacifica* in the following features: smaller size, thinner shell, radial ribbing on the left valve, winglike extension of the shell, and margin of commissural shelf not prominent in right valve.

Etymology: The specific name is for the abandoned village site of El Cuarenta that is in the vicinity of the type locality.

Occurrence: “Capay Stage” (middle lower Eocene). Bateque Formation, northwest of San José de Gracia area, Baja California, Baja California Sur, Mexico, CSUN locs. 1547, 1549, and 1575.

ACKNOWLEDGMENTS

Maria del Carmen Perrilliat (Instituto de Geología, Universidad Nacional Autónoma de México) arranged for paleontologic collecting and graciously provided type-specimen numbers. James H. McLean (Natural History Museum of Los Angeles County, Malacology Section) gave invaluable identification help and advice on the two new species of gastropods. Louella Saul (Natural History Museum of Los Angeles County, Invertebrate Paleontology Section) gave invaluable identification help with the *Dirocerithium* sp. specimens. Lindsey T. Groves (Natural History Museum of Los Angeles County, Malacology Section) shared his knowledge of *Gisortia*. Michael X. Kirby (University of California, Davis) provided an important reference on *Pycnodonte*. The manuscript benefited from the comments of two anonymous reviewers.

LOCALITIES CITED

CSUN 665. At elevation 2210 ft. along E side of small canyon, 861 m (2825 ft.) N and 709 m (2325 ft.) W of the SE corner of section 30, T6S, R13 E, U.S. Geological

Survey, 7.5-minute, Canyon Spring SW, California, quadrangle, 1963, northern Orocopia Mountains, Riverside County, southern California. Age: Middle early (“Capay Stage”). Collectors: R. L. Squires and D. M. Advocate, 1982.

CSUN 1220b. Along a prominent ridge, N side of a minor canyon on W side of Mesa La Salina, 84 to 130 m above the bottom of the exposures of the Bateque Formation in this area, 112°59'40"W and 26°44'40"N, coordinates 1.60 and 59.40 of Mexican government 1:50,000, San José de Gracia (number G12A64) topographic map, 1982, eastern Laguna San Ignacio area, Baja California Sur, Mexico. Age: Middle early Eocene (“Capay Stage”). Collector: R. L. Squires, 1993.

CSUN 1544a. Along E side of re-entrant on W side of Mesa La Salina, approximately 70 m above the bottom of the exposures of the Bateque Formation in this area, coordinates 4.35 and 55.70 of Mexican government 1:50,000, San José de Gracia (number G12A64) topographic map, 1982, eastern Laguna San Ignacio area, Baja California Sur, Mexico. Age: Early Eocene (“Capay Stage”). Collectors: R. L. Squires & R. A. Demetron, 1993.

CSUN 1544b. Approximately 30 m stratigraphically up-section from CSUN loc. 1544a. Age: Late early Eocene to early middle Eocene: Collectors: R. L. Squires & R. A. Demetron, 1993.

CSUN 1547. Approximately 17 km NW of village of San José de Gracia, at 120-m elevation near middle of east-facing cliff along canyon wall, near N end of Mesa La Azufrera, west side of Arroyo La Tortuga in vicinity of the abandoned village site of El Cuarenta, 112°53'13"W and 26°38'50"N, coordinates 12.45 and 48.80 of Mexican government 1:50,000, San José de Gracia (number G12A64) topographic map, 1982, Baja California Sur, Mexico. Age: Middle early Eocene (“Capay Stage”). Collectors: R. L. Squires & R. A. Demetron, 1992.

CSUN 1549. Approximately 15 km NW of village of San José de Gracia, near base of east-facing cliff and just W of dirt road, northern part of Mesa La Azufrera, W side of Arroyo La Tortuga, coordinates 14.7 and 48.1 of Mexican government 1:50,000, San José de Gracia (number G12A64) topographic map, 1982, Baja California Sur, Mexico. Age: Middle early Eocene (“Capay Stage”). Collectors: R. L. Squires & R. A. Demetron, 1992.

CSUN 1552. Approximately 5.5 km SW of the village of San José de Gracia, on W side of a narrow canyon at S end of Mesa San José, 112°45'15"W and 26°32'40"N, coordinates 26.20 and 36.95 of Mexican government 1:50,000, San José de Gracia (number G12A64) topographic map, 1982, Baja California Sur, Mexico. Age: Late early Eocene to early middle Eocene (“Domengine Stage”). Collectors: R. L. Squires & R. A. Demetron, 1992.

CSUN 1575. Approximately 18 km NW of village of San José de Gracia, along cliff face at S end of Mesa La

- Ladera just N of abandoned village site of El Cuarenta, coordinates 12.65 and 50.35 of Mexican government 1:50,000, San José de Gracia (number G12A64) topographic map, 1982, Baja California Sur, Mexico. Age: Middle early Eocene ("Capay Stage"). Collectors: R. L. Squires and R. A. Demettrion, 1993.
- LACMIP 461-B. "On the northern slope of a small canyon intersecting Las Lajas Canyon from the east" (Sutherland, 1966:1), U.S. Geological Survey, 7.5-minute, Santa Susana, California, quadrangle, 1951, north side of Simi Valley, Ventura County, southern California. Age: Late early to early middle Eocene ("Domengine Stage"). Collector: J. A. Sutherland, early 1960s?
- UCMO 7004. At elevation of 1700 ft. on a small cliff on S side of a side canyon to Las Lajas Canyon, 594 m (1950 ft.) N and 556 m (1825 ft.) E of SE corner of section 29, T3N, R17W, U.S. Geological Survey, 7.5-minute, Santa Susana, California, quadrangle, 1951 (photorevised 1969), north side of Simi Valley, Ventura County, southern California. Locality is in the informal "Stewart bed" and is equivalent to CSUN loc. 374 (Squires, 1984:58, 65). Age: Late early to early middle Eocene ("Domengine Stage"). Collector: R. L. Squires, 1981.
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Spawning, Larval Development, and Larval Shell Morphology of *Cantharidus callichroa callichroa* (Philippi, 1850) (Gastropoda: Trochidae) in Korean Waters

by

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Abstract. The present paper describes spawning, larval development and larval shell morphology of *Cantharidus callichroa callichroa* (Philippi) based on laboratory-reared materials. *C. callichroa callichroa* exhibits the typical features of benthic development of the genus, with lecithotrophic larvae that develop entirely within the egg mass attached to the hard substrate or algal fronds.

INTRODUCTION

Cantharidus callichroa callichroa (Philippi, 1850) (Family Trochidae, Subfamily Trochinae, Tribe Cantharidini) is a common small gastropod in the intertidal region of the rocky shore of Korea. Geographical distribution of this species is limited to the temperate region of the northwest Pacific (Habe, 1990).

Considerable work has been done on the early development and the larval shell morphology of marine gastropods, including species of *Cantharidus*, in order to (1) identify the larval shells (Kesteven, 1912; Robertson, 1971; Babio & Thiriot-Quiévreux, 1975) and (2) clarify the relationship between the developmental mode of a species and the morphology of its larval shell (Shuto, 1974; Turner et al., 1985; Colman et al., 1986; Colman & Tyler, 1988; Lima & Lutz, 1990; Hadfield & Strathmann, 1990). Lebour (1937) reported that *C. striatus* (Linnaeus) and *C. exasperatus* (Pennant) spawned the eggs as a gelatinous egg mass, and the young hatched at the crawling stage. With the aid of scanning electron microscopy, Babio & Thiriot-Quiévreux (1975) observed the shape of the protoconch and the first juvenile whorls of four species of *Cantharidus*: *C. clelandi* (Wood), *C. exasperatus*, *C. montagui* (Wood) and *C. striatus*. On the Pacific species of the genus *Cantharidus*, only a few reproductive and developmental studies have been done. Kojima (1961) studied copulating, spawning behavior and development of *C. cal-*

lichroa jessoensis (Shrenk); and Amio (1963) observed spawning mode of *C. japonicus* (A. Adams). Hadfield & Strathmann (1990) reviewed development of four species of trochid gastropods and questioned the usefulness of some inferred, but unobserved developmental characters, in the taxonomy of trochoideans. Recently, the diversity and variability in trochacean gastropods, including the genus *Cantharidus*, have been extensively reviewed by Hickman (1992).

The present paper describes spawning, larval development, and larval shell morphology of *Cantharidus callichroa callichroa* based on laboratory-reared materials.

MATERIALS AND METHODS

Adult *Cantharidus callichroa callichroa* were collected in the rocky intertidal zone of Pusan, Korea (35°06'N, 129°02'E) on 17 April 1991. They were transferred to the laboratory and maintained in glass bowls (4 L) at room temperature (16.0–20.0°C) with filtered seawater. They were fed red algae, *Acrosorium flabellatum* (Yamada), and *Carpopeltis cornea* (Okamura).

After spawning, the egg mass, attached to the alga *Carpopeltis cornea*, the only algal species submerged in the glass bowl by the authors, was removed from the rearing bowl and placed in a Petri dish (140 mm in diameter) containing filtered seawater.

Developing eggs were taken from the egg mass with a

fine forceps for microscopic observation. Magnesium chloride solution (Turner, 1976) was used as a relaxant for the juveniles. Egg diameter was measured along the maximum length; the size of protoconch was measured along the maximum dimension given by Lima & Lutz (1990). Drawings were made with the aid of a microscope equipped with a drawing tube. To document the spawning season and peak spawning period, field observations on the Pusan population were made from February to July 1991.

RESULTS AND DISCUSSION

In the field, *Cantharidus callichroa callichroa* spawned a gelatinous egg mass on submerged rocks or the fronds of algae such as *Carpopeltis cornea*, *Pachymeniopsis elliptica* (Holmes), and *Acrosorium flabellatum*. The egg masses were found from April to July, and the peak was observed in mid-May. In the laboratory, the egg mass spawned was attached to the surface of the glass bowl or on fragments of algal fronds by the snail. The egg mass was yellowish, transparent, and amorphous, with a somewhat elongated globular shape (Figure 1A); maximum length was ca. 1.5 cm. The wrinkled or furrowed surface was sparsely covered with benthic diatoms or debris (Figure 2B). The outermost gelatinous layer was sticky and elastic, but became stiff when exposed to air in low tide. The gelatinous slime of the egg mass presumably functions, not as nutritive material, but as protective layer only, as suggested by Thorson (1946), because the slime remains disfigured and torn even after hatching.

Eggs were spawned in weak strings (Figure 1A, B) embedded in the gelatinous egg mass. The strings are easily disrupted by mild handling or weak pressure, and therefore often broke into pieces within the egg mass (Figure 1A). The egg mass (or egg-binding jellies in Hickman, 1992), however, is attached to the substrate, firmly persisting through all of development. The same characteristics of the egg-binding jellies were reported in *Cantharidus exasperatus* by Fretter (1984). The number of eggs per egg mass varied from approximately 1000 to 1500. The size of the uncleaved eggs varied from 353 μm to 533 μm (mean = 446 μm ; SD = 48; n = 30). A globular shaped egg was enclosed with three jelly coatings (Figure 1C): (1) the egg membrane (em), (2) the inner jelly coating (ij), and (3) the outer jelly coating (oj), which is quite transparent. It could not be detected without careful treatment and high magnification ($> \times 400$). These layers enclosing the egg are identical to that of *Calliostoma ligatum* (Gould) (Family Trochidae) described by Strathmann (1987). In *Calliostoma granulatum* (Born), however, only two coats are reported by Ramon (1990): (1) an egg membrane (em) and (2) a mucus sheath, but the presence of egg membrane was not clearly presented in that paper. This complex jelly coating of *C. callichroa callichroa* is an additional example of a unique derived feature of Superfamily Trochacea proposed by Hickman (1992).

The gastrula phase (Figure 1D) finished in a few hours within the egg membrane.

In the post-torsional veliger (after first 90 degrees of torsion) (Figure 1E), we can observe a relatively small and simple lobe-shaped velum with cilia, the yellowish and globular shaped digestive glands, and the right larval retractor muscle. Veligers rotate backward by the movement of the ciliated velum within the egg membrane. The post-torsional veliger (after second 90 degrees of torsion) (Figure 2A, B) retains a considerable mass of the digestive glands, which are still present in the crawling, young stage after metamorphosis. Young animals, therefore, are able to survive for a few days after hatching without any feeding. At this stage, the eye and the digitate cephalic tentacles were observed. The teleoconch started growing, and, at this stage, the complete loss of the velum took place within the egg membrane (Figure 2C). The whole of torsion and metamorphosis occurred within the egg membrane (Figure 2C) prior to hatching. The fact that the teleoconch started growing at this stage within the egg membrane is consistent with the observations of Lima & Lutz (1990) that early development of the teleoconch was common in some prosobranch gastropods which have non-planktonic larval stages.

The juveniles hatched at 16.0–20.0°C as well-developed crawling animals about seven days after spawning in the laboratory (Table 1). The hatching time was considerably shorter than that of other trochids with benthic developmental mode such as *Margarites marginatus* Dall (20–23 days at 8.5–9.0°C; 10–15 days at 11.0°C) (Hadfield & Strathmann, 1990); however, this may result from development at a much warmer temperature.

The isostrophic, inflated protoconch (Figure 2D–F), which consists of approximately 1.25 whorls with a blunt apex, is somewhat clear, colorless, unornamented, and coarsely grained in its outer surface. The number of whorls and the surface features are very similar to those of other species of *Cantharidus* (*C. clelandi*, *C. exasperatus*, *C. montagui*, and *C. striatus*) studied by Babio & Thiriot-Quievreux (1975). The orthostrophic teleoconch (Figure 2D–F), which is clearly distinguished from the protoconch, exhibits a series of ridges (seven to eight in number) crossed by weak growth lines. This morphology is similar to those of the above mentioned *Cantharidus* species. To quantify the comparative morphology of the protoconch, Shuto (1974) proposed the ratio of maximum diameter (D) to the number of the whorl (vol.). He reported that the ratio was 0.3–1.0 in the non-planktonic development of prosobranchs. According to Shuto's scheme, the ratio (D/vol.) of *Cantharidus callichroa callichroa* is 0.3. The size of the protoconch is 238–312 μm (mean = 288 μm ; SD = 15; n = 22). The size is within the range of the average size (230–500 μm) of prosobranch species that have non-planktonic larvae (Jablonski & Lutz, 1983). Hadfield & Strathmann (1990), however, stated that "for species with inflated pausispiral protoconchs, conclusions as to whether development is pelagic or benthic cannot be drawn reliably

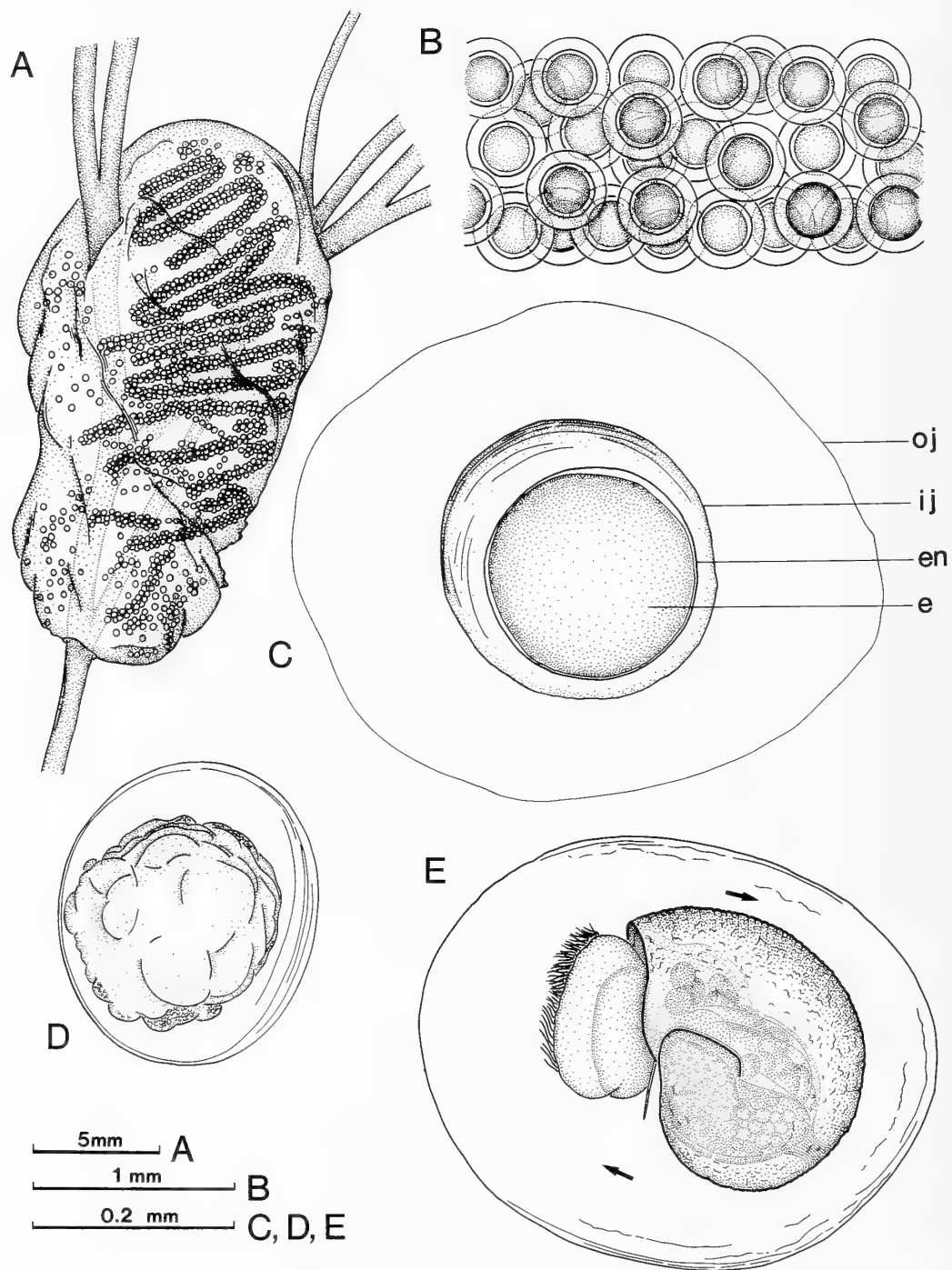


Figure 1

Cantharidus callichroa callichroa (Philippi) A. An egg mass attached to the algae, *Carpopeltis cornea*. B. A part of the egg string. C. An uncleaved egg showing the structure of egg coverings (e, egg; em, egg membrane, ij, inner jelly coating; oj, outer jelly coating). D. A gastrula stage. E. A left side view of the post-torsional veliger stage (after first 90 degrees of torsion) (dg, digestive glands; lrm, larval retractor muscle; op, operculum; vl, velum). The arrows indicate a direction of rotation.

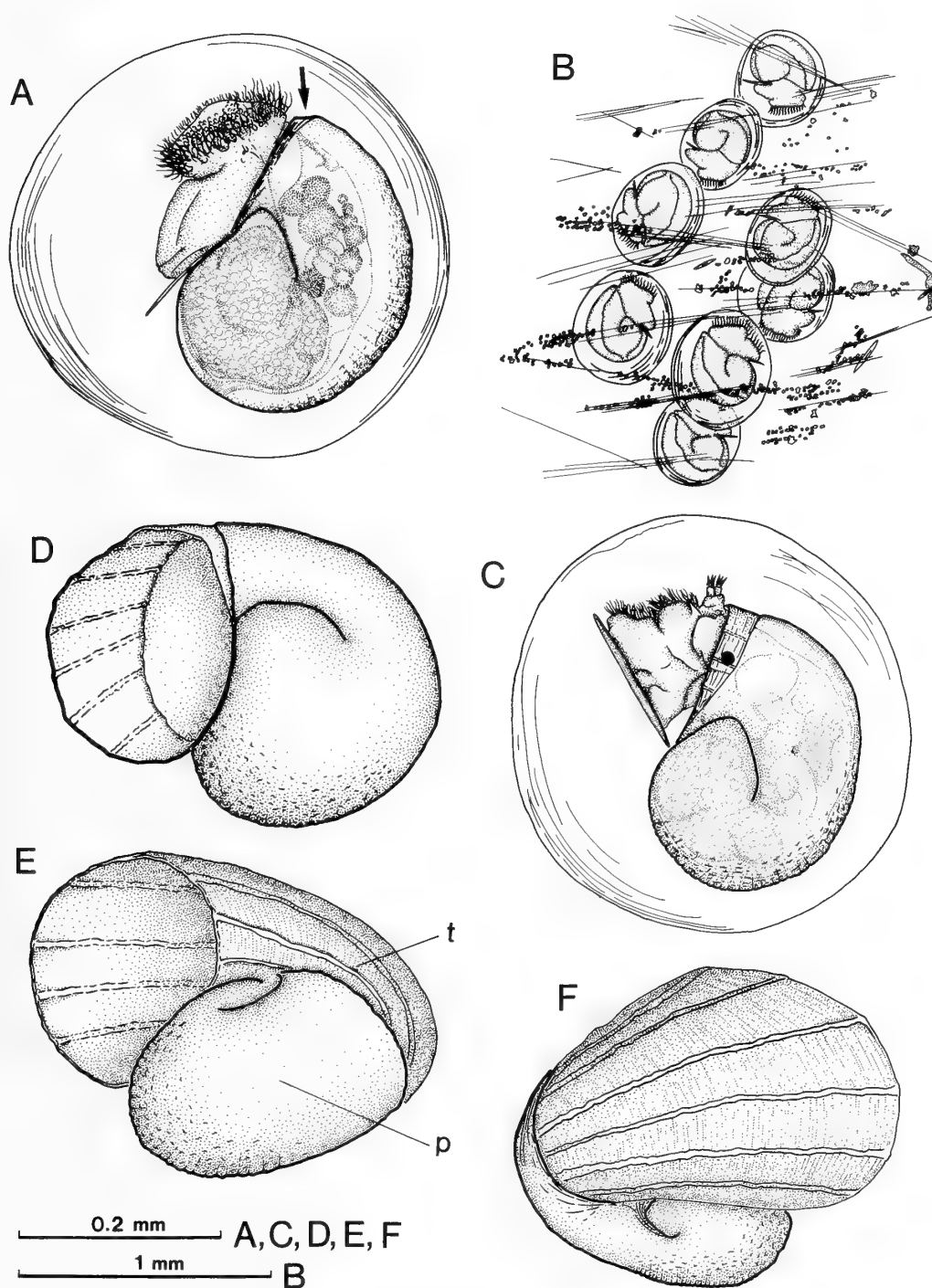


Figure 2

Cantharidus callichroa callichroa (Philippi) A. A left side view of post-torsional veliger stage (after second 90 degrees of torsion). The arrow indicates the teleoconch. B. A part of the egg mass containing late veliger larvae. C. A left side view of the juvenile stage just before hatching. D. A ventro-lateral view of the larval shell just after hatching. E. A ventro-lateral view of the larval shell (t, teleoconch; p, protoconch). F. A dorso-lateral view of the larval shell.

Table 1

Chronology for the embryonic development of *Cantharidus callichroa callichroa* at 16.0–20.0°C in the laboratory.

Time after fertilization	Developmental stage
3 hours	4-cell stage
5 hours	16-cell stage
20 hours	gastrula stage
41 hours	young veliger with lobe-shaped ciliated velum within the egg membrane
7 days	crawling juvenile with a foot and a shell

from what is known of development in related species.” Hickman (1992) reported that “popular classification of molluscan developmental modes and strategies are not useful because they underestimate the range of variation in trochacean development.” The present study provides an additional example of benthic developmental mode in the species of *Cantharidus*.

These results show that *Cantharidus callichroa callichroa* bears the typical features of benthic development of the genus, with lecithotrophic larvae that develop entirely within the egg mass attached to a hard substrate or algal fronds.

ACKNOWLEDGMENTS

We thank Dr. D. Jablonski, Department of Geophysical Sciences, University of Chicago, who read the manuscript critically. We are especially grateful to anonymous reviewers for upgrading the manuscript. Korea Research Foundation has supported page charges. This is contribution No. 342 from the Korea Institute of Ocean Science (KIOS), National Fisheries University of Pusan.

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Descriptions of Four New Eulimid Gastropods Parasitic on Irregular Sea Urchins

by

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Abstract. *Hypermastus mareticola* is described from Guam, *H. orstomi* from New Caledonia, both parasitizing the heart urchin *Maretia planulata*. *Hypermastus obliquistomum* Warén, 1991 is recorded from the sand dollar *Laganum depressum* from New Caledonia (host species not recorded previously). *Eulima encopicola* is described from the Galapagos Islands, parasitizing the sand dollar *Encope micropora galapagensis*. *Balcis clypeastericola* Habe, 1976, parasitic on the clypeasteroid sea urchin *Clypeaster japonicus* in Japan, is made the type species of a new genus, *Clypeastericola* and a new species *C. natalensis* lives on *Clypeaster eurychoreus*, from southeastern Africa. Two further records of species of *Clypeastericola* are recorded from *Clypeaster australasiae* (Gray), from New South Wales, and from *Laganum depressum* from New Caledonia, but the species are left undescribed.

INTRODUCTION

Eulimid gastropods are not frequently collected on their hosts unless the echinoderms are specifically searched and handled with care; most eulimids have the capacity to voluntarily leave (and many do it regularly) the echinoderms on which they are feeding. Therefore, the most profitable way to find eulimids is by intertidal collecting, where one can see them directly when picking up the echinoderms, and they do not have the time to pull out their proboscis and drop off the host.

Occasionally, eulimids are found as a side result of other investigations when hosts are collected, especially eulimids permanently attached to their hosts. This paper is based on such material sent to the senior author for identification. The material presented here is not extensive, but it improves our knowledge of the groups, especially the host-parasite relations. Here we describe one new genus and four new species which parasitize "irregular" sea urchins.

There are very few records and specimens of such eulimids (Warén & Crossland, 1991).

A complication of eulimid nomenclature which concerns the species parasitic on irregular sea urchins was the introduction of an ichnogenetic name, *Heckerina* (Alekseev & Endelman, 1989). This was created for some holes, diameter 1.0-2.3 mm, in tests of Cretaceous specimens of *Galerites orbiculatus* (d'Orbigny, 1854) (Irregularia, Galeritidae). They were assumed to have been caused by eulimid gastropods.

MATERIALS AND METHODS

The material used for this paper is enumerated under each species. It is now deposited, usually together with voucher specimens of the hosts, in museums listed under "Material examined." The number of available specimens was too small to allow much more than a description of the shell, except of *Hypermastus mareticola* Warén & Norris, sp.

nov., of which a few specimens were serially sectioned for anatomical study. (Those results will be reported later.)

Author names of the new species are to be quoted as in the headings for each species.

SYSTEMATICS

Family EULIMIDAE Philippi, 1852

Hypermastus Pilsbry, 1899

Hypermastus Pilsbry, 1899:258. Type species: *H. coxi* Pilsbry, 1899, by original designation, Australia, New South Wales, Port Stephens. Host not known.

Remarks: Warén & Crossland (1991) reviewed the species assumed or known to belong to *Hypermastus*. Eleven species are known to live on irregular sea urchins in tropical regions. Habe (1992) has since described one species from an echinothurid sea urchin from Japan, *Hypermastus araeosomae* Habe, 1992, but that species differs from the others by having a light yellow shell, and since very little else is known about it, we consider the systematic position provisional.

The two new species described below are also questionable members of *Hypermastus*, but presently there is no genus available where they fit better.

Hypermastus mareticola Warén & Norris, sp. nov.

(Figures 1–3)

Type material: Holotype and four dry and six alcohol-preserved paratypes in Division of Mollusks, U.S. National Museum of Natural History, Washington D.C., register numbers 860367, 860369, and 860368; six paratypes in Swedish Museum of Natural History, register numbers 4531.

Type locality: Guam, Apra Harbor, about 10 m depth, parasitic on *Maretia planulata* (Lamarck, 1816) (Spatangidae, Spatangoida). (Voucher specimens USNM E 43011).

Material examined: One snail, attached on host (16 mm diameter), Apra Harbor, 10 m, 16 August 1992. Fifteen additional hosts on which snails had been observed in the field but had fallen off during collection or preservation were also studied, and the distribution of the snails on the host is given in Figure 3. A total of 10 snails were obtained from these. In all, 21 snails were collected from hosts during June, July, and August, 1992, all at the type locality.

Etymology: Named after the generic name of its host.

Description: (Based on supposed females.) Shell (Figure 1A–E) tall, slender, greyish-transparent, almost perfectly smooth. The larval shell (Figure 1F) is colorless, cylindrical, mucronate, obliquely inserted, with slightly more than 1.5 whorls and a height of 300–320 μ m. The holotype has 7.0 distinctly convex teleoconch whorls, with a very shallow and inconspicuous suture. There are seven rather

evenly distributed incremental scars with intervals of 0.7–1.3 whorls. The scars are very thin and not conspicuously deepened, except close to the apical suture. There is no sculpture except some incremental unevenness in the shell which hardly deserves the term “incremental lines.” The subsutural zone is conspicuous, and its height corresponds to about 25% of the height of the whorl. The aperture is pear-shaped, rather tall, with a distinct parietal callus, but no distinct angle between the parietal wall and columella. The outer lip is very slightly prosocline, retracted at the suture and most protruding just apically to the mid-point.

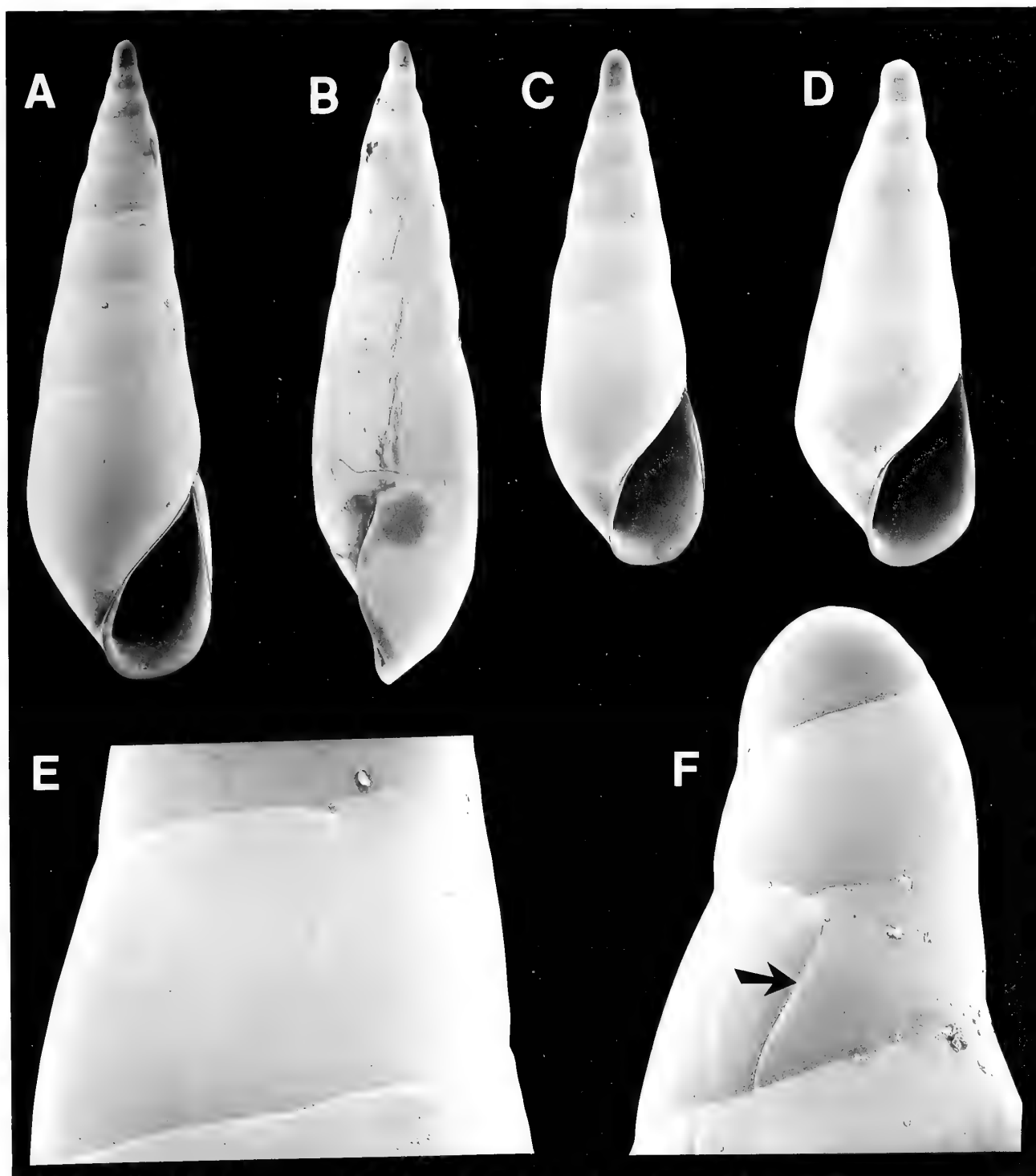
Male. (Figure 1C) about 60% of the height of the female and slightly more slender.

Dimensions. Eighteen mature specimens collected June–August 1992 had the following shell heights: 5.20, 5.00, 4.72, 4.64, 4.40, 4.24, 4.04, 3.96, 3.76, 3.72, 3.24, 3.16, 3.00, 2.92, 2.80, 2.56, 2.52, 2.52 mm. Four immature specimens (recognized by the angular periphery of the body whorl, Figure 1D) were 4.60, 2.56, 1.88, 1.88 mm. The height of the holotype is 4.40 mm, its breadth is 2.52 mm.

Soft parts. The eyes are large, 80 μ m in diameter, and situated 200 μ m apart, basally at the outside of the tentacles. The tentacles are tapering, slightly longer than the distance between the eyes. The proboscis is fully retractile. The foot is larger than the opercular lobes and has a distinct propodium. In preserved specimens, it is displaced toward the right side. The operculum fills the aperture and is very thin and colorless with no reinforcing ribs or special muscular attachments. Five specimens of the following sizes were decalcified for serial sectioning: 5.2 mm, 5.0 mm, 4.6 mm (supposed females and immature female), 3.2, and 3.0 mm (supposed males). The two large specimens and the one of intermediate size all had oviducts but lacked a penis. The two small specimens assumed to be males had a penis. The sex of these specimens was confirmed at serial sectioning and examination of the gonad.

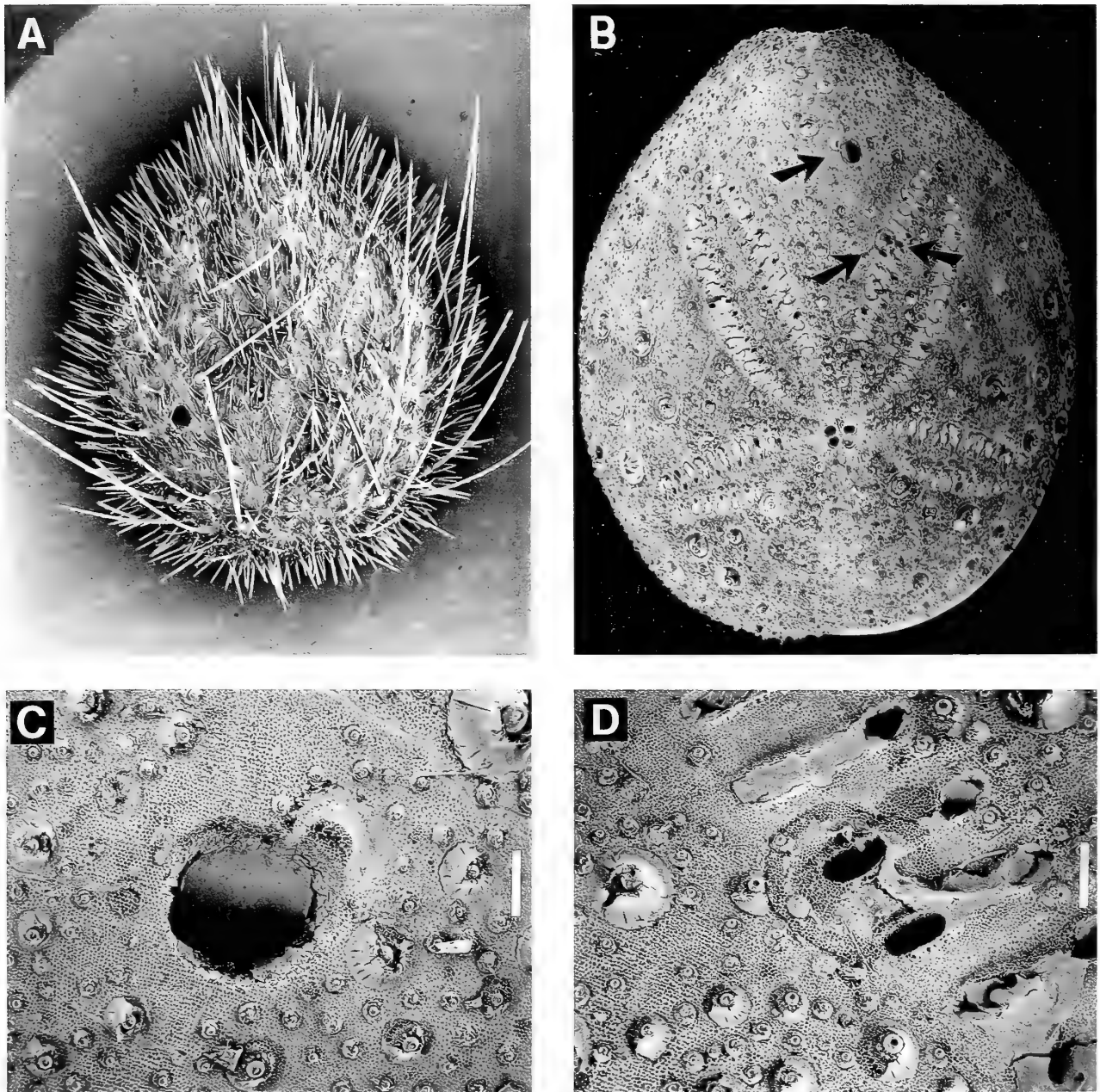
Remarks: *Hypermastus mareticola* was found on its host in connection with ecologic work on *Maretia planulata* and *Metalia dicrana* H. L. Clark, 1917 (Brissidae) in Guam. Although these two heart urchins occur microsympatrically, the eulimid was found only on the former species. Some details of the ecology of the host were described by Norris (1992).

One snail was still attached on its host (16 mm diameter) by pinching two pedicellariae between its operculum and peristome. It was positioned dorsally over the right posterior ambulacrum, about 5 mm from the gonopores and between the two double rows of tube-feet. A small area, about 0.8 mm diameter, was slightly discolored, darker brown, with a hole from the proboscis in the center. Inside the host, there was a corresponding discolored, slightly swollen area, but no indication that the proboscis had gone farther, as to the gonads. There was no proboscis of the parasite protruding from the hole, and no torn proboscis could be seen on the snail, which indicates that it is fully retractile.



Explanation of Figure 1A-F

Figure 1A-F. *Hypermastus mareticola* Warén & Norris, sp. nov., syntypes. A-B. 4.6 mm (female?). C. 2.8 mm (male?). D. 1.9 mm (young female?). E. Incremental scar, length 380 μ m. F. Larval shell, height 310 μ m.



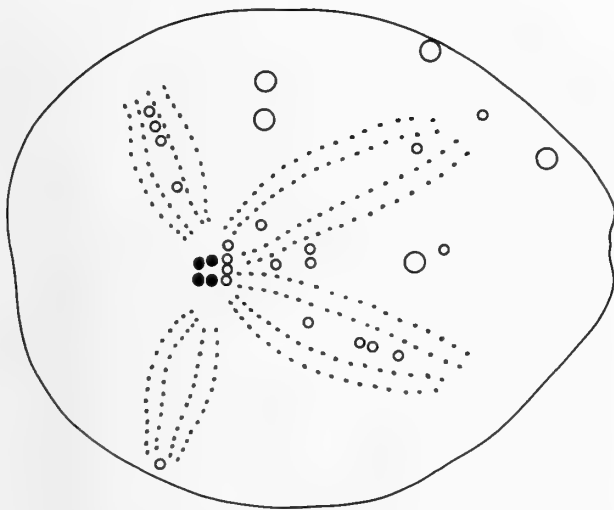
Explanation of Figure 2A-D

Figure 2A-D. *Maretia planulata*, with damages of test from being parasitized by *Hypermastus mareticola* Warén & Norris, sp. nov. (marked by arrows). A. Diameter of test 11.6 mm diameter (excl. spines). B. 17.4 mm diameter. C. Large hole on specimen B, diameter 0.5 mm. D. Small scar around a hole of a tube foot. Scale bar 0.25 mm.

A rough estimate is that 10-25 percent of the host specimens were infested; and 20 percent of the parasitized specimens of *Maretia planulata* had more than one snail, with a maximum of four snails on the single host.

The 15 host specimens represented in Figure 3 had a total of 25 holes from proboscides. Two of the holes seemed to be healing. Ten specimens of the parasite were saved,

which means either that 15 specimens were lost (which is possible), or that the snail frequently changes host or position on the host, and leaves a hole on the host. We cannot say which of these possibilities best explains the discrepancy, perhaps it is a combination. All snails had been attached aborally on the test, and their distribution is plotted in Figure 3. This figure indicates that they prefer the



Explanation of Figure 3

Figure 3. Distribution of holes and scars made by *Hypermastus mareticola* Marén & Norris, sp. nov. on 15 specimens of *Maretia planulata*, on which the eulimid was found. The size of the hosts (10–18 mm test diameter) has been standardized to make comparisons possible. Large circles indicate large holes (Figure 2C).

leeward side, perhaps to avoid getting scraped off when the sea urchin is moving forward in the sediment.

The distinction between males and females from shell characters is tentative; it is rare to obtain eulimids in quantities large enough to allow impeccable statistics, especially since the procedure is destructive. Nevertheless, we find it worth drawing attention to this assumed sexual dimorphism.

Hypermastus mareticola is not a very characteristic species, but the cylindrical, mucronate larval shell drastically reduces the number of genera from which to choose. It bears some resemblance to *Balcis echinocardiaphila* Habe, 1976 (Figure 5A–B), a species parasitic on the heart urchin *Echinocardium cordatum* (Pennant) in Japan (not on *Spatangus purpurea* as quoted in Warén & Crossland, 1991). That species is, however, considerably larger, about 13 mm, and has a more ovate aperture. No soft parts have been described from *Balcis echinocardiaphila*, which makes comparison difficult. It is likely that they will end up in the same (new) genus in the future.

Hypermastus orstomi Warén, sp. nov.

(Figures 4A–E)

Type material: Holotype and two paratypes in Laboratoire de Biologie des Invertébrés Marins et de Malacologie, Museum National d'Histoire Naturelle, Paris.

Type locality: New Caledonia, Lagon de Noumea, Grande Rade, 22°15.26'S, 166°23.98'E, 11–12 m depth, sand with ooze on surface, 14 April 1993, three specimens attached dorsally on *Maretia planulata* (P. Bouchet, Labora-

toire de Biologie des Invertébrés Marins et de Malacologie, Museum National d'Histoire Naturelle, Paris).

Material examined: Only known from the type material.

Etymology: Named after L'Institut Français de Recherche Scientifique pour le Développement en Coopération, formerly Office de la Recherche Scientifique et Technique Outre-Mer (ORSTOM), whose personnel in Noumea has sent the senior author numerous new and interesting eulimids with host information.

Description: (Sex not known.) The shell (Figure 4A–C) is short, stout, conically ovate, colorless, transparent, with mucronate apex and large aperture. Protoconch 1 (Figure 4B) is colorless, and has 1.7 perfectly smooth whorls with very indistinct suture. Its height is about 250 μ m but varies according to how much is concealed by the subsequent whorl. There is no protoconch 2. The holotype has 8.0 perfectly smooth, very flat whorls with a few indistinct incremental lines, mainly restricted to the subsutural zone, and two to four slightly stronger incremental scars. The suture is barely visible, the false suture more distinct, and the subsutural zone occupies one-fifth to one-sixth of the height of the whorls. The peristome is rather oblique, pear-shaped, slender, and somewhat expanded in its lower part. Seen in profile, the outer lip is prosocline, retracted at the suture and most protruding just apically to its mid-point.

Dimensions. Height of holotype 5.89 mm.

Remarks: Since only three specimens were available, it was not possible to examine the soft parts (this requires that the shell is dissolved). The few cases available show that *H. orstomi* causes unusually little disturbance of the test of the host. A few spines had fallen off around the point of attachment apically within one of the petals, and the area around was slightly darker than its surroundings.

Hypermastus orstomi is broader and shorter than most eulimids, especially those assigned to *Hypermastus*. *Hypermastus coxi* has similar proportions between breadth and height, but is more cylindrical with much more rapidly expanding apical teleoconch whorls (see Warén & Crossland, 1991, fig. 4A–F). Species of *Turveria* (see Warén & Crossland, 1991, figs. 9H–I, 10A–B) have a similar shape of the shell, but an apically more constricted aperture and a color pattern on the shell.

Hypermastus obliquistomum Warén, 1991

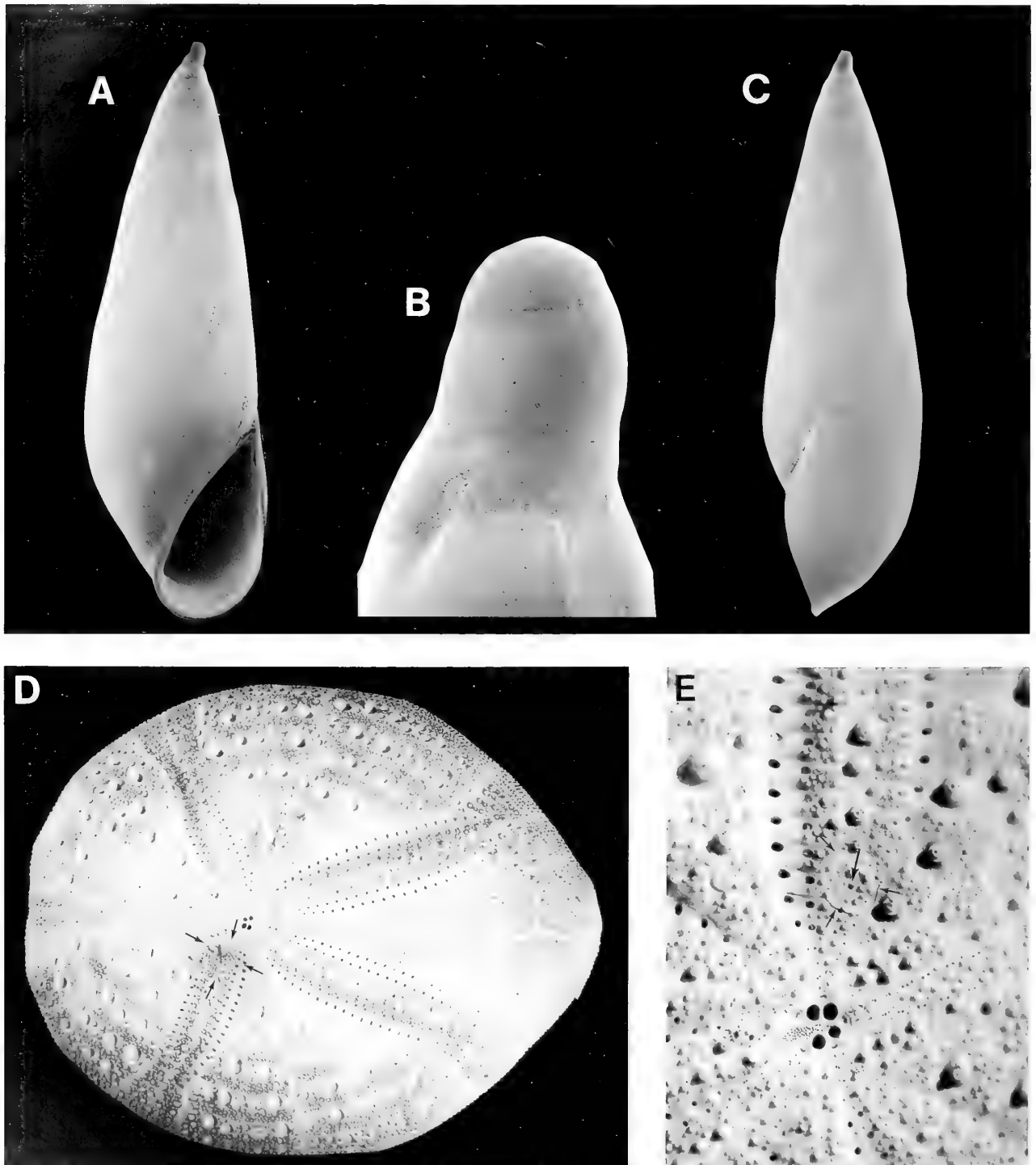
(Figure 6A–F)

Hypermastus obliquistomum Warén, in Warén & Crossland, 1991:100, figs. 7E, 7F, 12H.

Type material: Holotype, Australian Museum, Sydney, c.160815.

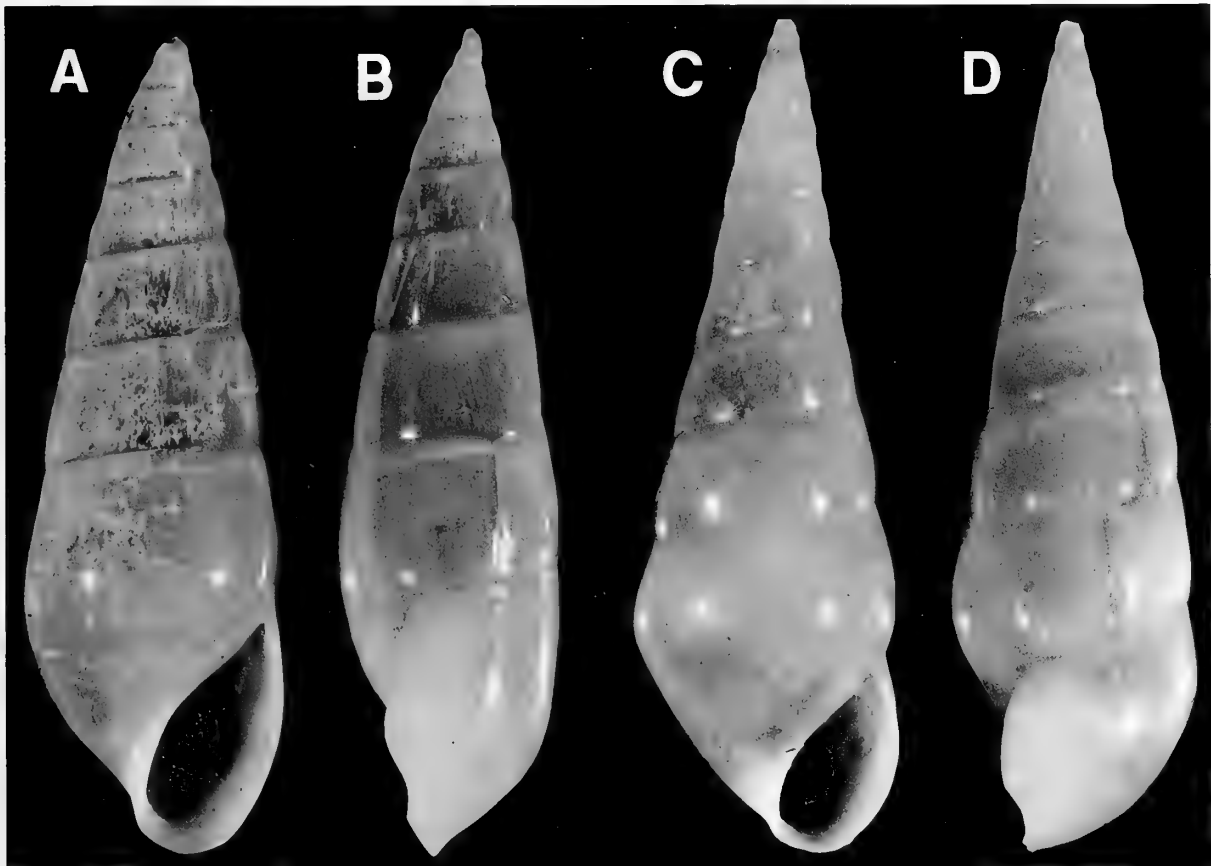
Type locality: From oral side of "sand dollars," Mud flat, Baie des Isoles, Noumea, New Caledonia.

New material: Northern New Caledonia, N/O Alis station DW 1181, 19°23.9'S, 163°14.7'E, 45 m, 31 October



Explanation of Figure 4A-E

Figure 4A-E. *Hypermastus orstomi* Warén, sp. nov. and its host *Maretia planulata*. A, C. Paratypes, height of shells 5.5 mm. B. Protoconch, height 240 μ m. D. Aboral view of test, host of one specimen of *Hypermastus orstomi* Warén, sp. nov. Area of attachment indicated by fine arrows. Diameter of test 46 mm. E. Enlargement of central part of test, showing apical area with four gonopores and the area of attachment (fine arrows) for the proximal part of the proboscis. Penetration of test (diameter 0.1 mm) marked by slightly larger arrow. Horizontal width of picture 7 mm.



Explanation of Figure 5A-D

Figure 5A-B. "*Balcis*" *echinocardiaphila* Habe, syntypes National Science Museum, Tokyo, register number 52460, height of shell 13.1 and 11.9 mm respectively. C-D. *Clypeastericola clypeastericola* (Habe), syntype, National Science Museum, Tokyo, register number 52468, height of shell 14.2 mm.

1989, one specimen attached orally on *Laganum depressum* L. Agassiz, 1841 (Laganidae); New Caledonia, Lagoon de Noumea, Quatre Bancs de l'Ouest, 22°25.36'S, 166°27.77'E, 12 m depth, sand bottom with *Halimeda* and *Sargassum*, 10 *L. depressum* parasitized on oral side among ca. 350 specimens examined 19 April 1993 (P. Bouchet, Laboratoire de Biologie des Invertébrés Marins et de Malacologie, Museum National d'Histoire Naturelle, Paris).

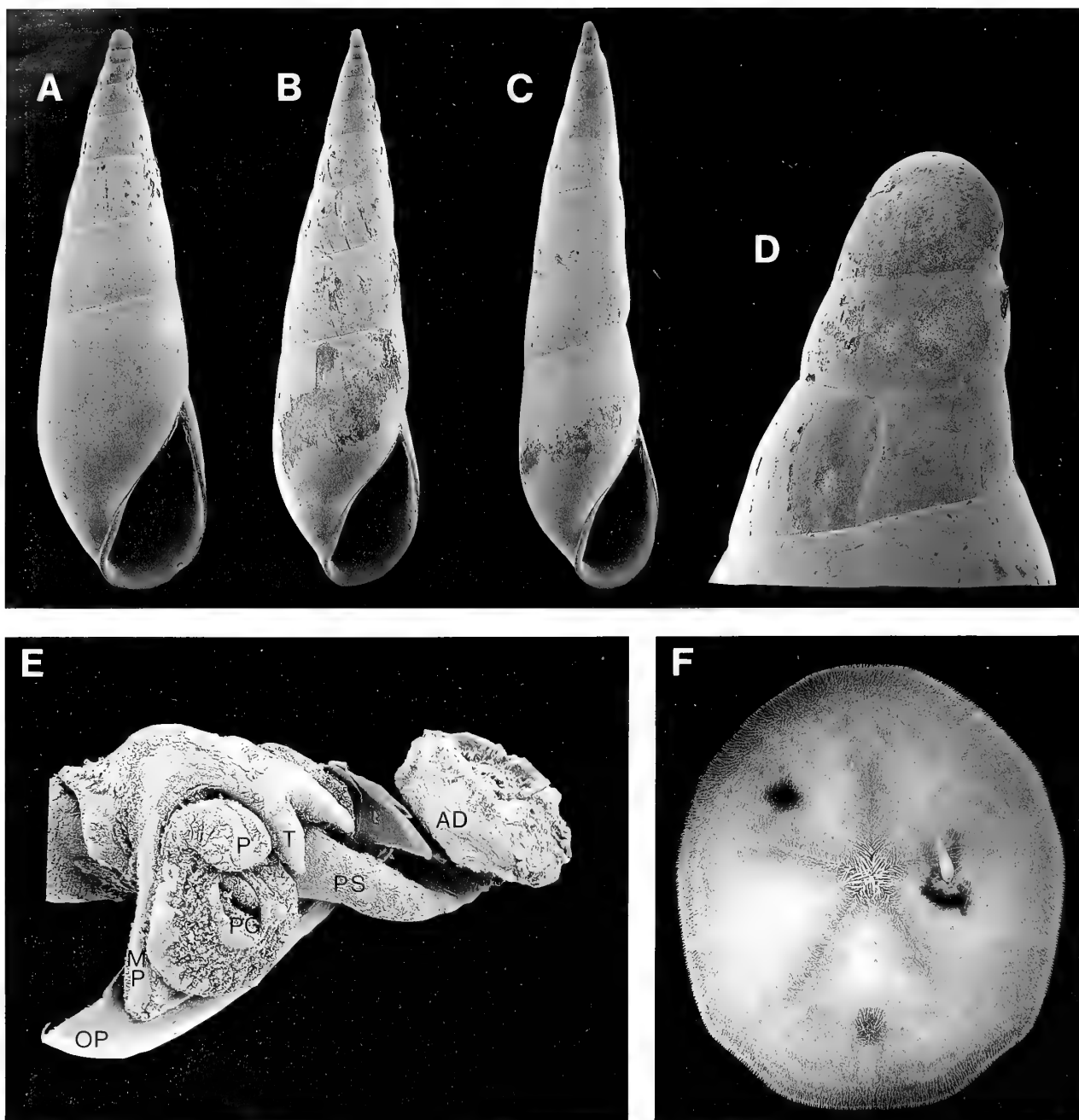
Distribution: Only known from the holotype and the present specimens, all from New Caledonia.

Remarks: This species was previously known from the holotype, found on an unidentified sand dollar from New Caledonia. The new material makes it possible to give some additional information and to describe the morphology of the head-foot, which is rather small but functional. The tentacles are long, smooth, regularly conical, with large black eyes in indistinct lateral bulges on the sides of the bases. The inner sides meet centrally over the proboscis opening. The foot is small, broader posteriorly, with an inconspicuous propodium and a large and conspicuous

opening for the posterior pedal gland. The metapodium forms a conspicuous ridge on the right side and an almost tongue-shaped flap on the left side, considerably larger than the left one. The proximal part of the proboscis sheath is large and voluminous and ends with a sucker-shaped disc which is used to attach the snail to the test of the host. From the underside of this disc exits the much more slender distal part of the sheath, which penetrates the test, is highly extensible, and may be extended two or three times the length of the shell.

Two specimens had originally been parasitizing the host collected in 1989, close to each other (Figure 6E), but one of them had evidently been torn off or left the host. When Warén received the specimen, the second specimen had also fallen off.

Of the 10 hosts collected in 1993, eight hosts had a single scar, one had two, and one had three scars, which means that the observed rate of infestation by more than one specimen is considerably higher than a random distribution admits. The size range of the 11 specimens (two were lost when collected) is 8.1–5.8 mm; a single specimen measures



Explanation of Figure 6A-F

Figure 6A-F. *Hypermastus obliquistomum* and its host *Laganum depressum*. A. Assumed male 4.2 mm high. B. Female, 8.3 mm high. C. Assumed secondary female, 6.4 mm high. D. Larval shell, height 370 μ m. E. Critical point dried head-foot of *H. obliquistomum*; pallial skirt and visceral mass removed. Width of foot 0.25 mm. F. *Laganum depressum*, oral side with *H. obliquistomum*. Diameter of test 60 mm. AD—attachment disc of proboscis; MP—metapodial (opercular) fold; OP—operculum; P—propodium; PG—posterior pedal gland; PS—proximal part of proboscis sheath; T—cephalic tentacles.

4.15 mm. Among the larger ones, there is a distinct dimorphism in shell shape, some specimens being considerably more slender (Figure 6C). One specimen of each type was decalcified and sexed. The less slender one was a female, the more slender one was also determined to be a female, but with a vestigial penis. Both specimens had well-developed pallial oviducts. This may indicate that some specimens develop directly to females, while others pass through a male period.

The sites of attachment are indicated by narrow holes in the test with a diameter of about 0.1 mm. The hole is surrounded by a scar where the proboscis sheath has been attached, and a much larger, 4–8 mm diameter, surface which is denuded of spines and somewhat blackened. The scar from the sucker is usually surrounded by a dark, small mucus collar.

A host specimen with one empty scar and one specimen of *H. obliquistomum* still attached was dissected, and there were still slender proboscides remaining inside the test, under both holes, both of them ending freely in the cavities of the gonads.

The thick, proximal part of the proboscis can evidently be retracted inside the cephalic haemocoel and must therefore be considered a part of the proboscis sheath, not a snout, which it could be mistaken for when examined in an everted state. The damage of the test of the host indicates that at least the females stay for a considerable period of time on the same spot and only occasionally leave the host.

Hypermastus obliquistomum resembles *H. colmani* Warén, 1991, presumed to parasitize *Peronella leseuri* (Valenciennes, 1841) (Laganidae) in Australia. That species does, however, differ in having a taller protoconch with three convex whorls and a height of 0.46 mm.

Eulima Risso, 1826

Eulima Risso, 1826:123. Type species: *Turbo subulatus* Donovan, 1804 (= *Eulima glabra* (Da Costa, 1778)) (Warén 1992; ICZN, Opinion 1718), European. Parasitic on ophiuroids.

Remarks: The generic name *Eulima* has been used for a broad range of eulimids in the literature, but Warén (1983) gave some information about the type species and a very similar species, *E. bilineata* Alder. These species have a ptenoglossate radula, used for catching coelomocytes in the coelomic cavities of the hosts (unpublished). The new species below differs in parasitizing a sand dollar echinoid and in lacking a radula. Otherwise it is very similar, in shell characters and in being a hermaphrodite of some kind. We have therefore decided to keep this species in *Eulima*, although it is likely that it will need a new genus.

Eulima encopicola Warén & Templado, sp. nov.

(Figures 7A–E)

Type material: Holotype and the single paratype in Mu-

seo Nacional de Ciencias Naturales, Madrid, Spain, register number 15.05/6958.

Type locality: Galapagos Islands, Santiago Island (James Island), Sullivan Bay, Bartolome inlet. 19 March 1991. On a specimen of *Encope micropora galapagensis* A. H. Clark, 1946 (Encopidae), the larger one, holotype, (4.76 mm) attached on the oral side; the smaller one (3.04 mm) on the aboral side.

Description: Shell (Figure 7A–D) tall, conical, slender, transparent with some brownish color in the subsutural zone and on the body whorl. The larval shell (Figure 7E) is blunt, evenly rounded, not obviously colored, consists of slightly more than one whorl and has a height of 330 μ m. The holotype has 7.5 almost flat teleoconch whorls, sculptured with distinct, sharp, close-set, but not very uniformly spaced incremental lines, and six irregularly spaced incremental scars (Figure 7D) of varying strength. The subsutural zone is conspicuous, and its height corresponds to about 25% of the height of the whorl. The aperture is tall and slender with a sturdy columellar callus and a thin parietal callus, which together form a distinct angle. The apical corner of the aperture is distinctly drawn out and constricted. The outer lip is slightly damaged in the holotype, but has evidently been very straight and is slightly prosocline.

Dimensions. Height of holotype 4.76 mm, diameter 1.40 mm.

Operculum. Very thin, fragile and colorless with no reinforcements.

Soft parts. The soft parts (preserved in alcohol) have a pinkish hue. The large specimen has a well-developed oviduct and penis; the small one only a penis. The eyes are unusually small, diameter about 20 μ m and situated about 100 μ m apart. No other details were seen since the specimens were dried and reconstituted to facilitate the extraction of the soft parts for radular preparation. The anterior pedal gland is very large and invades the cephalopodal haemocoel. No radula was found in any of the specimens.

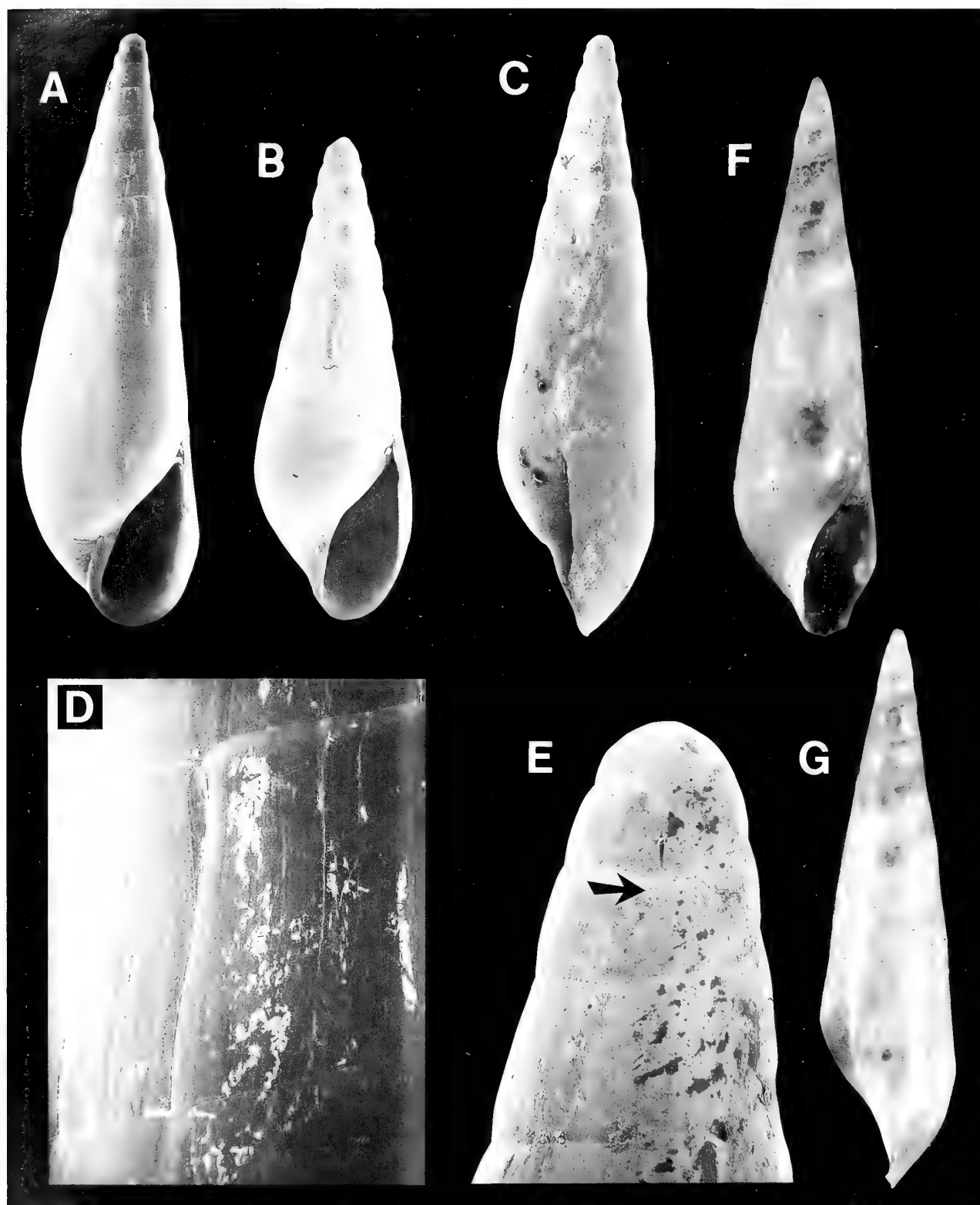
Etymology: Named after the generic name of its host.

Remarks: *Strombiformis barthelowi* Bartsch, 1917 (Figure 7F–G), from the Gulf of California, is of a similar size and shape, but the initial whorl of the protoconch (I) is very small, the larval shell is distinctly conical with 2–3 whorls, and the whole shell is indistinctly yellowish (not easy to see in the holotype because of the remaining dried soft parts).

Clypeastericola Warén, gen. nov.

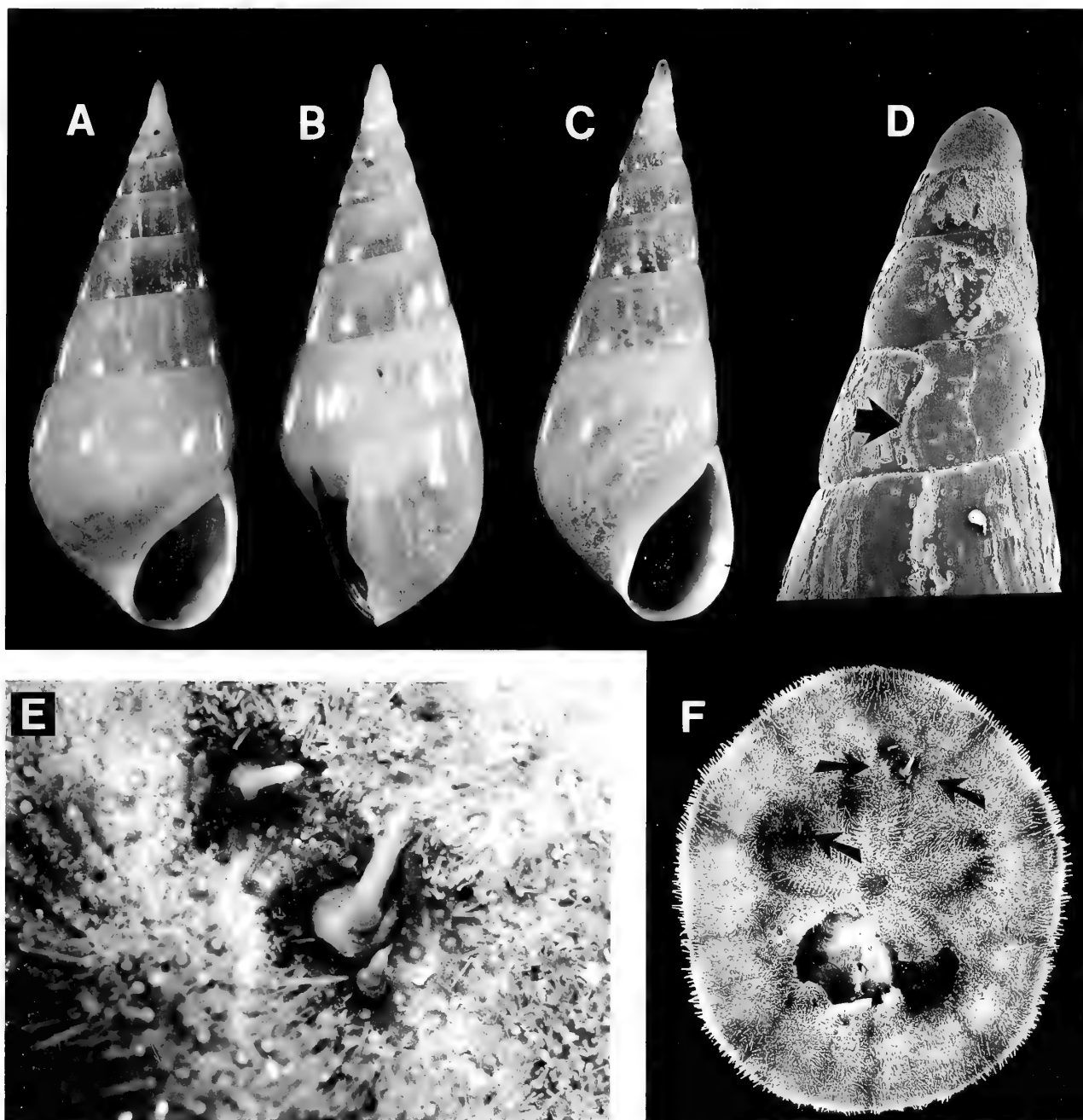
Type species: *Balcis clypeastericola* Habe, 1976, from Japan (Figure 5C–D), parasitic on *Clypeaster japonicus* Doederlein, 1885 (Clypeasteridae).

Diagnosis: Eulimids with a colorless, slender, smooth, and conical shell. Aperture low, constricted in female, less so



Explanation of Figure 7A-G

Figure 7A-E. *Eulima encopicola* Warén & Templado, sp. nov. A, C. Holotype (female?), height of shell 4.76 mm. B. Paratype, 3.04 mm. D. Incremental scar, length 0.75 mm. E. Larval shell, labial scar indicated by arrows, height of protoconch 330 μ m. F-G. *Eulima barthelowni* (Bartsch), holotype, USNM 268622, height of shell 4.93 mm.



Explanation of Figure 8A-F

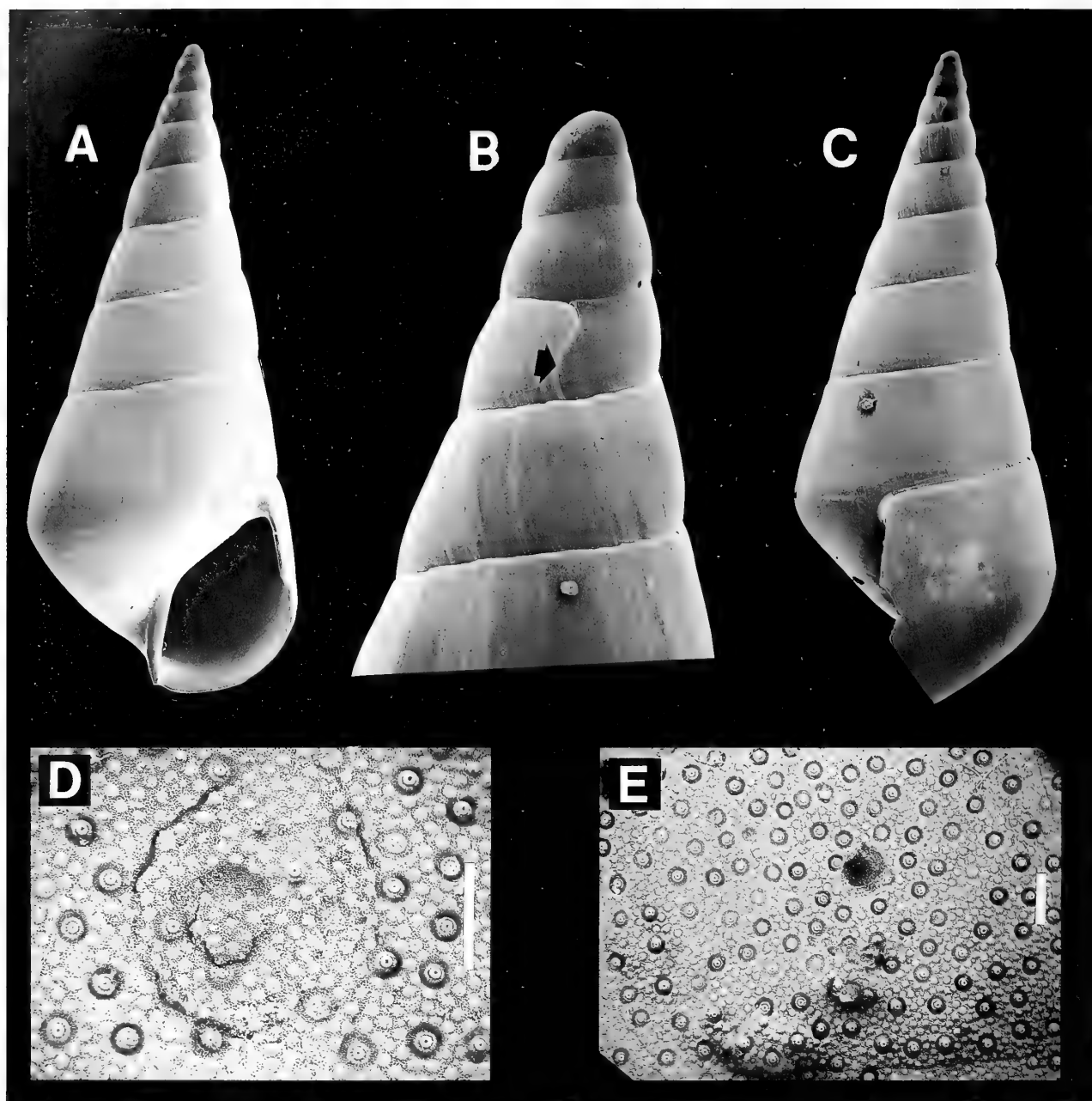
Figure 8A-F. *Clypeastericola natalensis* Warén, sp. nov. and its host *Clypeaster eurychoreus*. A. Holotype (female?), 6.4 mm. B. Young female, 3.9 mm. C. Male, 4.7 mm. D. Larval shell marked with an arrow. Height 460 μ m. E-F. Host, *Clypeaster eurychoreus*, diameter 41 mm, with remaining proboscides of a group of one female and two males and a second female. E. Detail of F, showing the torn off proboscides.

in male. Proboscis with an attachment disc, more developed in female.

Etymology: Named after *Clypeaster*, the host genus for at least three species.

Remarks: The diagnosis above is based on the shell of *C.*

clypeastericola and *C. natalensis* but on the soft parts of *C. natalensis*, since *C. clypeastericola* has been available only as empty shells. The shells are, however, very similar, and we feel certain that they are congeneric. The similarity in the shape of the aperture of the females, a small dip in the suture, and a corresponding constriction of the peri-



Explanation of Figure 9A-E

Figure 9A-E. *Clypeastericola* sp. and scars on its host *Clypeaster australasiae*. A, C. Height 4.9 mm. B. Larval shell, height of protoconch 520 μ m. D-E. Details of test of *Clypeaster australasiae* with scars from *Clypeastericola* sp. Scale lines 1 mm.

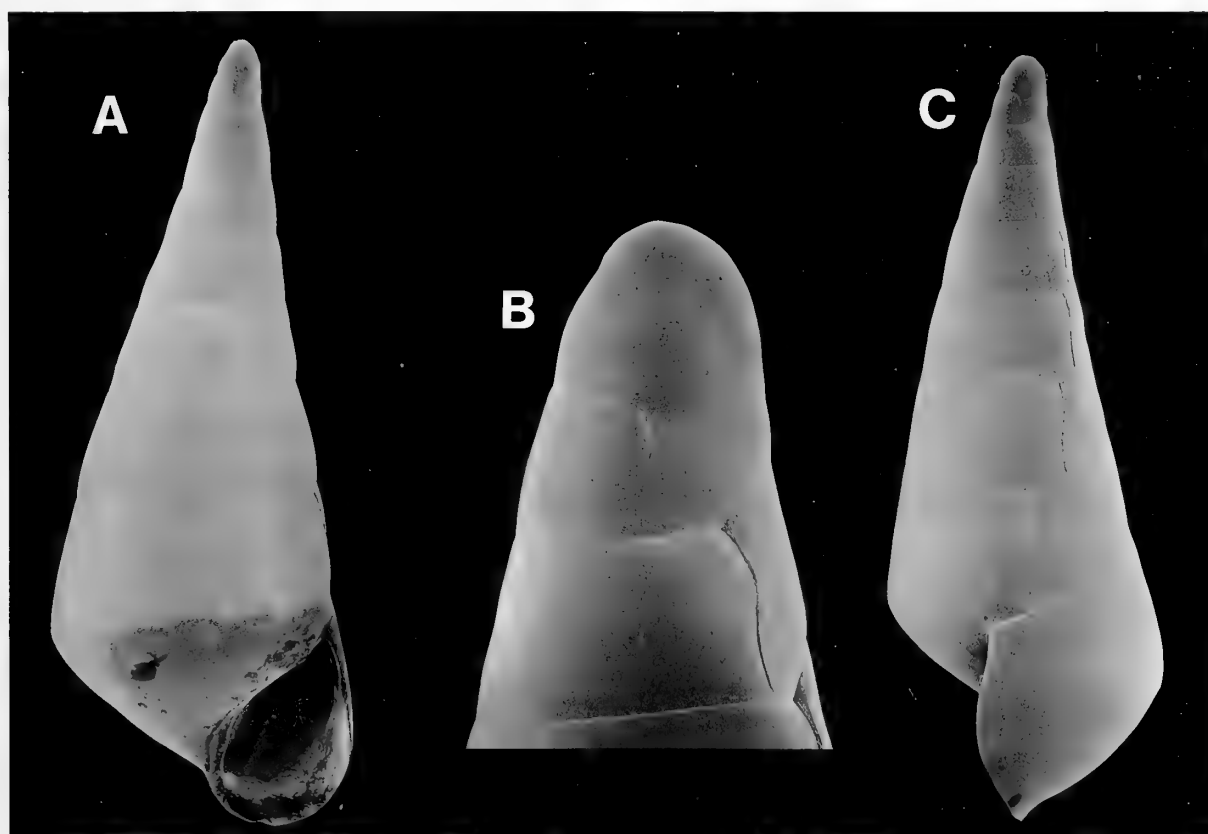
stome is a rare feature, obvious only in the genus *Parvioris* Warén 1981. Those species have an operculum with a fold that is deeply inserted in the foot, and they are parasitic on asteroids.

The two undescribed species discussed below have similar shells but are immature, judging from the angular periphery of the body whorl.

Clypeastericola natalensis Warén, sp. nov.

(Figures 8A-F)

Type material: Holotype, a female, Natal Museum, Pietermaritzburg, register number NMP D 8634/T841; three paratypes, one immature female and two males, S7878/T842.



Explanation of Figure 10A-C

Figure 10A-C. *Clypeastericola* sp. from *Laganum depressum*. A. Front view, 4.0 mm high. B. Protoconch, height 350 μ m. C. Side view, height 3.8 mm.

Type locality: Eastern South Africa, Northern Zululand, southeast of Kosi Estuary, 26°24.1'S, 32°34.8'E, 50 m, fine sand. 08 June 1987, on a small *Clypeaster eurychoreus* Clark, 1924 (Clypeasteridae). One immature female was attached alone, one adult female was accompanied by two males. Position, see Figure 8F.

Etymology: Named after the Natal province.

Description: Shell (Figure 8A-C) conical, rather inflated, whitish semitransparent, rather solid, smooth and shiny. The conical, tall, and pointed larval shell (Figure 8D) consists of about three whorls and its height is 460 μ m. The mature female has 8.5 slightly convex whorls. The suture is deep and conspicuous; the false suture is poorly defined and hardly noticeable. The female has two incremental scars, 1.1 and 2.2 whorls from the outer lip. The shell has some irregular and indistinct growth lines and a very irregular and weak spiral striation. The aperture is short and broad, slightly contracted. The parietal callus is well-developed, but there is no distinct angle between the parietal wall and the columella. The outer lip is slightly retracted at the suture and very slightly prosocline.

Dimensions. Height of the holotype 6.39 mm, breadth 2.44 mm.

Male. Shell slightly more slender and with a single incremental scar about one whorl from the outer lip. Height 3.88 and 4.64 mm.

Operculum. Rather thin, slightly yellowish, with a distinct reinforcement rib on the inside.

Soft parts. (Of immature female.) The oviduct is beginning to develop as a more solid zone along the right corner of the pallial cavity. The tentacles are long and tapering with large eyes, 100 μ m diameter and 200 μ m apart, placed well behind the cleavage between the tentacles. The foot is small, smaller than the opercular lobes. The right side of the anterior part of the head-foot has an epipodial fold ending at the proboscis opening. The metapodium bulges out widely at both sides of the foot; the right one is connected to the right epipodial fold. The propodium is well-developed. There is no trace of a penis.

The proboscis is firmly attached to the test of the host (Figure 8E), over a hole of a tube-foot, which is used for penetrating the test. All proboscides were so firmly attached that they had been torn off, above the attachment

disc. This disc is much broader in the female than in the male. The proboscis of the young female ended freely in the coelomic cavity. The proboscis of the large female was inserted between the coelomic epithelium and the test for 10 mm until reaching a gonad, which was penetrated.

Remarks: Probably the epi- and metapodial folds can be used to cover the base of the shells to avoid irritation of the host, but the specimens had nevertheless caused some damage on the test, which was denuded around the snails.

Clypeastericola natalensis differs from *C. clypeastericola* in having a shorter and proportionally broader shell (cf. Figures 8A–C and 5C–D).

Clypeastericola spp.

(Figures 9A–E, 10A–C)

Material examined: (Species 1.) Australia, New South Wales, off Port Hacking, on *Clypeaster australasiae* (Gray, 1851) (Clypeasteridae), taken by a trawler, one young specimen attached to test, AMS C 108275.

(Species 2.) New Caledonia, Lagon de Noumea, Grande Rade, 22°15.26'S, 166°23.98'E, 11–12 m, sand with ooze on surface, 14 April 1993, two immature specimens attached on aboral side of *Laganum depressum* (P. Bouchet, Laboratoire de Biologie des Invertébrés Marins et de Malacologie, Museum National d'Histoire Naturelle, Paris).

Remarks: The test of the Australian host had three perforations (two figured in Figure 9D–E), indicating that it had been the host of at least that number of specimens. The remaining one is figured in Figure 9A–C.

The New Caledonian species differs in being more slender with flatter whorls and in having a smaller protoconch with less than two whorls (almost three in the Australian specimen).

We find these young specimens worth mentioning but not naming. The shells are quite similar to the two species of *Clypeastericola* described above, and contribute to the reasons for this introduction of a new name.

ACKNOWLEDGMENTS

We thank the Malacology sections at the Museum National D'Histoire Naturelle, Paris, the Australian Museum, Sydney, and the Natal Museum, Pietermaritzburg, South Africa, who contributed specimens for this study. Christine Hammar, Stockholm, prepared Figure 3 and the prints used for the plates. R. Rabago, P. Rabago, and C. I. Norris (Guam) assisted in the collection of specimens in Guam. This is Contribution 344 from the University of Guam Marine Laboratory.

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Review of the Genus *Hallaxa* (Nudibranchia: Actinocyclusidae) with Descriptions of Nine New Species

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Abstract. The genus *Hallaxa* previously included five described species. This paper describes nine new species of *Hallaxa*, and reviews the morphology of three of the previously described species. *Hallaxa atrotuberculata*, *H. albopunctata*, *H. iju*, *H. elongata*, *H. translucens*, *H. paulinae*, *H. hileenae*, and *H. cryptica* are described from the Indo-Pacific tropics, while *H. michaeli* is from the temperate east coast of Australia. The anatomy of an additional Indo-Pacific species is described, but the species is not named, as it is known only from preserved material. The polarity of characters is evaluated and a preliminary phylogeny is presented. The relationship of *Hallaxa* to *Actinocyclus*, the Chromodorididae, and other doridaceans is discussed.

INTRODUCTION

The genus *Hallaxa* Eliot, 1909, was originally erected to include two species, *H. decorata* (Bergh, 1878) and *H. indecora* (Bergh, 1905), both from the Indo-Pacific tropics. Subsequently, three species have been described, all from subtropical and temperate regions: *Hallaxa apesfai* Marcus, 1957, from the subtropical coast of Brazil, *H. chani* Gosliner & Williams, 1975, from the Pacific coast of North America; and *H. gilva* Miller, 1987, is known from New Zealand.

Recent collections by several workers in the Indo-Pacific tropics have included specimens of several new species of *Hallaxa* (Figure 1). This paper describes the morphology of these species, as well as an additional species from temperate Australia, and reviews the anatomy of several previously described species. This review also permits a discussion of morphological variation in *Hallaxa* and a preliminary phylogenetic analysis.

Material from several institutions was examined during this study. Abbreviations for these institutions are as fol-

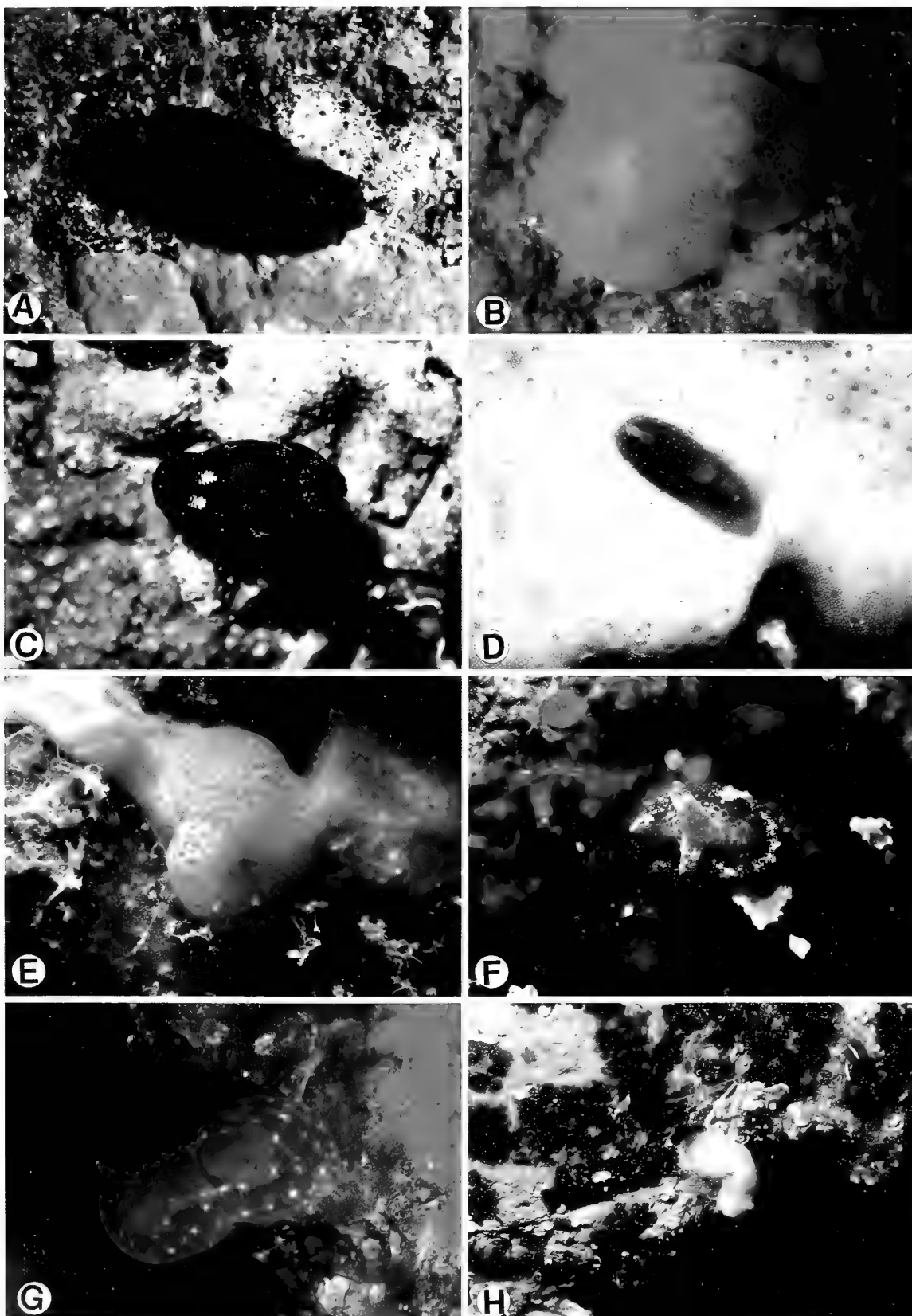
lows: AM, Australian Museum, Sydney; BPBM, Bernice P. Bishop Museum, Honolulu; CASIZ, California Academy of Sciences, San Francisco; SAM, South African Museum, Cape Town; USNM, National Museum of Natural History, Washington.

SPECIES DESCRIPTIONS

Hallaxa Eliot, 1909

Type species: *Halla decorata* Bergh, 1878, by original designation. *Hallaxa* was a replacement name for *Halla* Bergh, 1878, a junior homonym of a genus of polychaete annelid.

Diagnosis: Body fleshy, without spicules, ovoid, elliptical or round. Color variable. Most species cryptic on sponge prey. Rhinophores perfoliate, bulbous or rarely conical. Gills unipinnate, 6–14 in number, retractile. Anterior margin of foot straight or concave. Oral tentacles present or modified to oral pits. Jaws armed with undivided or multifid rodlets. Radula without rachidian row of teeth.



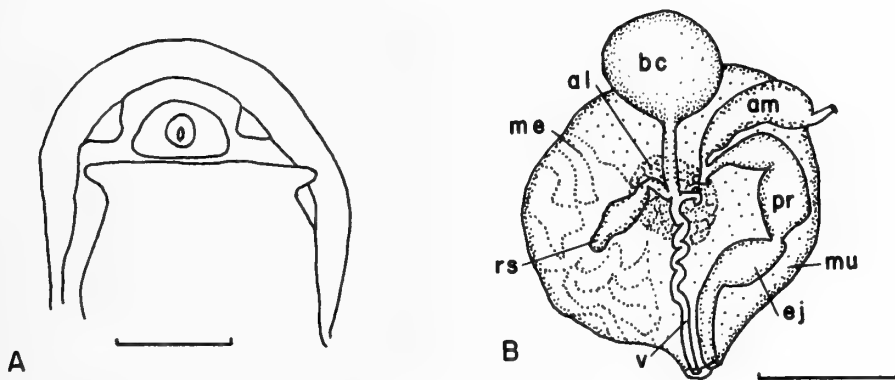


Figure 2

Hallaxa aepae Marcus, 1955. A. Line drawing of ventral view of head, drawn by camera lucida from preserved specimen, scale = 0.5 mm. B. Reproductive system, al- albumen gland, am- ampulla, bc- bursa copulatrix, ej- ejaculatory portion of the vas deferens, me- membrane gland, mu- mucous gland, pr- prostatic portion of vas deferens, rs- receptaculum seminis, v- vagina, scale = 0.5 mm.

Inner lateral teeth broad, denticulate. Outer lateral teeth thin, bearing multiple denticles. Each half row of radula containing 4–22 outer lateral teeth per half row. Reproductive system triaulic. Vas deferens prostatic proximally, ejaculatory more distally. Receptaculum seminis semiserial in arrangement, situated opposite or distal to uterine duct. Membrane gland separate or united with remainder of female gland mass. Penis simple, unarmed.

Hallaxa aepae Marcus, 1957

(Figures 2, 3)

Hallaxa aepae Marcus, 1957:421, figs. 73–80.

Material: One specimen, CASIZ 066166, dissected, Brazil, courtesy of Dr. Eveline Marcus. The specimen was labelled “paratype,” but the original description was based on a single specimen, which was dissected. The present specimen has no formal systematic status, and no locality information was contained with the specimen. It is likely that the specimen was collected from the type locality.

Distribution: This species is known only from the type locality, Ubatuba, Brazil.

External morphology: The living holotype animal described by Er. Marcus (1957) was 7 mm long. It was light yellowish gray with darker viscera showing through the translucent notum. A series of tubercles extended mid-

dorsally from the head to anterior of the branchial plume where they divide and encircle the gills. The present preserved specimen is 7 mm long. Only a trace of the original raised tubercles remains. The body is broad and rounded. The rhinophores have nine lamellae, and there are nine unipinnate gills. The anterior margin of the foot (Figure 2A) is straight with laterally extending anterior foot corners. A pair of triangular lappets is present on the anterior side of the head.

Internal morphology: The labial cuticle consists of numerous rodlets (Figure 3A) with one to four denticles along their free margin. The radular formula was $30 \times 9-11.1.0.1.9-11$ in the holotype and $31 \times 10.1.0.1.10$ in the present specimen. The inner lateral teeth (Figure 3B, C) are broad and thick. The free end of the teeth bears six to seven denticles. The innermost denticle is largest, and they diminish in size outwardly. The outer lateral teeth are narrow and elongate (Figure 3D). The innermost outer lateral tooth bears eight to nine elongate denticles along its inner edge.

The reproductive system (Figure 2B) is triaulic. The pre-ampullary duct is narrow and short. The ampulla is short and wide. It narrows and divides into the short oviduct and the vas deferens. The vas deferens expands into a folded prostatic portion. The prostatic portion narrows to a constriction and again expands into a wide muscular portion that narrows and terminates at the common genital

Figure 1

Living animals. A. *Hallaxa atrotuberculata* Gosliner & Johnson, sp. nov., photo by T.M.G. B. *Hallaxa translucens* Gosliner & Johnson, sp. nov., photo by T.M.G. C. *Hallaxa iju* Gosliner & Johnson, sp. nov., photo by T.M.G. D. *Hallaxa elongata* Gosliner & Johnson, sp. nov., photo by T.M.G. E. *Hallaxa paulinae* Gosliner & Johnson, sp. nov., photo by Pauline Fiene-Severns. F. *Hallaxa hileenae* Gosliner & Johnson, sp. nov., photo by T.M.G. G. *Hallaxa cryptica* Gosliner & Johnson, sp. nov., purple form, photo by T.M.G. H. *Hallaxa michaeli* Gosliner & Johnson, sp. nov., photo by Michael Gosliner.

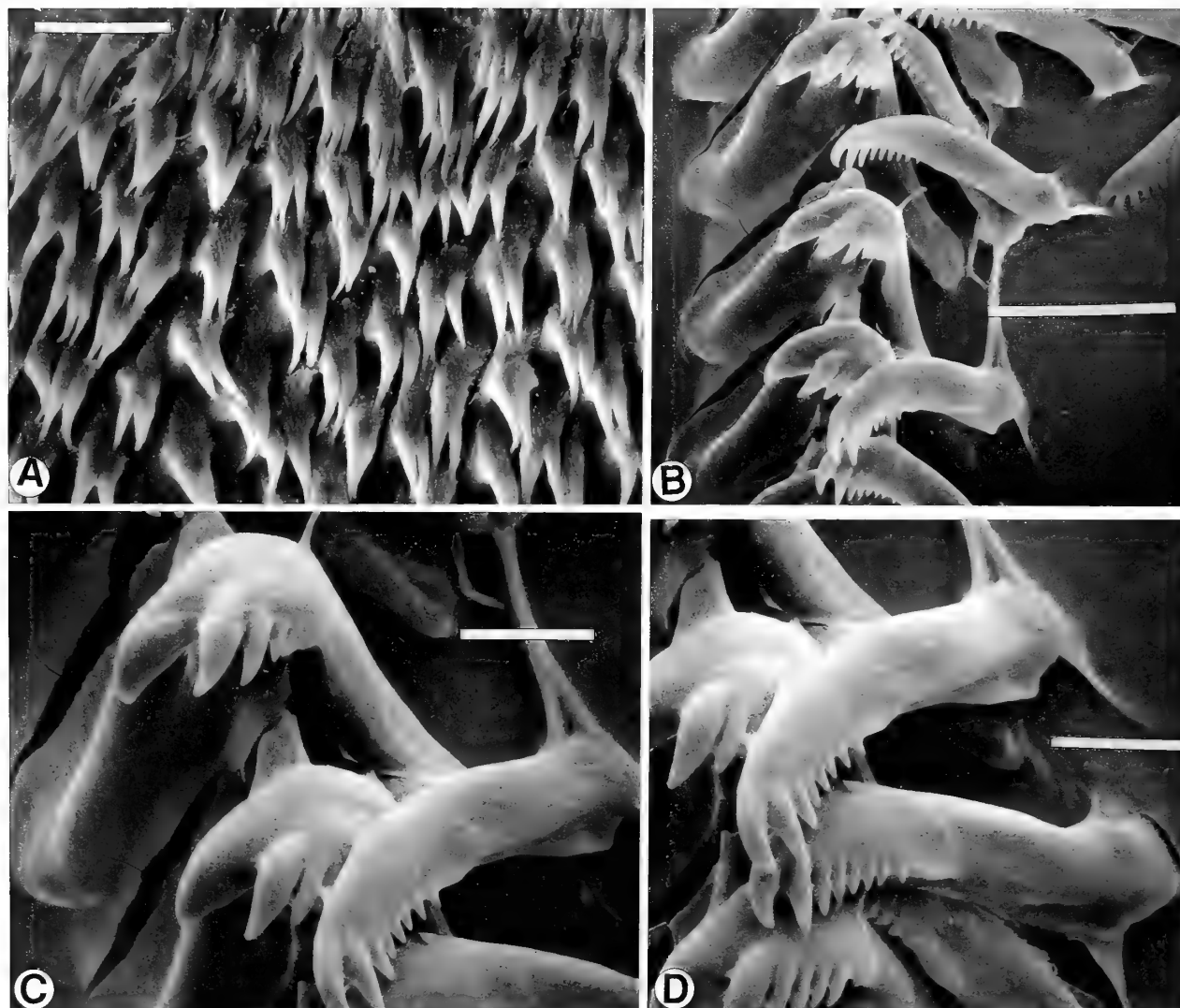


Figure 3

Hallaxa aepae Marcus, 1955. Scanning electron micrographs. A. Jaw rodlets, scale = 10 μm . B. Inner lateral and adjacent outer lateral teeth, scale = 25 μm . C. Inner lateral teeth, scale = 10 μm . D. Innermost outer lateral teeth, scale = 10 μm .

opening. The vaginal opening is immediately adjacent to the proximal termination of the vas deferens. The vagina is narrow and elongate. It includes several loops and has a common junction with the ducts of the bursa copulatrix, receptaculum seminis, and the uterine duct. The receptaculum seminis is pyriform and elongate. The bursa copulatrix is large and spherical. The female gland mass is composed of three portions, the albumen, membrane, and mucous glands.

Discussion: The specimen examined here is virtually identical to the morphology originally depicted by Er. Marcus (1957). The only significant difference is the absence of a vaginal diverticulum and the more proximal position of

the uterine duct in the present material. The uterine duct is situated at the juncture of the receptaculum seminis with the vagina. As no other species of *Hallaxa* has the vaginal diverticulum, it is doubtful that Marcus actually observed this structure in the holotype.

Hallaxa aepae is relatively plesiomorphic in its anatomy and can be distinguished from all other species by having a mid-dorsal, longitudinal line of tubercles that divides and encircles the gills.

Hallaxa chani Gosliner & Williams, 1975

(Figures 4, 5)

Hallaxa chani Gosliner & Williams, 1975:396, figs. 2-8.

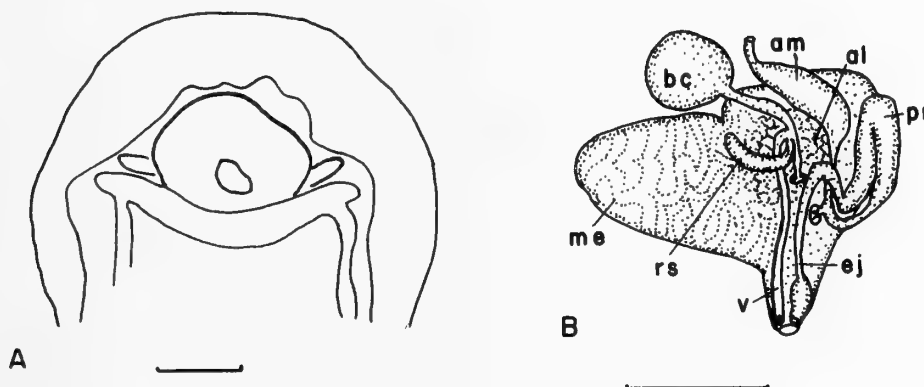


Figure 4

Hallaxa chani Gosliner & Williams, 1975. A. Line drawing of ventral view of head and foot of preserved specimen, drawn with camera lucida, scale = 1.0 mm. B. Reproductive system, al- albumen gland, am- ampulla, bc- bursa copulatrix, ej- ejaculatory portion of vas deferens, me- membrane gland, mu- mucous gland, pr- prostatic portion of vas deferens, rs- receptaculum seminis, ud- uterine duct, v- vagina, scale = 0.5 mm.

Material: Paratype radula, CASIZ 020376. One specimen, CASIZ 070787, dissected, intertidal, North Shell Beach, San Luis Obispo County, California, 31 December 1971, G. McDonald.

Distribution: This species is known along the Pacific coast of North America from Grant Island, Ketchikan, Alaska to San Luis Obispo County, California (Behrens, 1991).

External morphology: The living animals are translucent yellowish with numerous dermal brown patches showing through the translucent notum. The body is broad and rounded. The notum is covered with scattered rounded tubercles. The rhinophores have 9–10 lamellae. The branchial plume is composed of 12–14 unipinnate gills. The anterior end of the foot (Figure 4A) is fairly straight with elongate extensions of its anterior corners. A short, digitiform tentacle is present on either side of the mouth.

Internal morphology: The labial cuticle is situated within the anterior end of the buccal mass. It is composed of numerous multifid rodlets. The radular formula is $30 \times 13.1.0.1.13$ and $31 \times 14.1.0.1.14$ in two specimens examined. The inner lateral teeth (Figure 5C, D) are broad, but narrower than those of other species studied here. The free margin of the inner laterals bears a single large cusp on its inner side with four to eight smaller denticles on the outer side. The outer laterals are narrow basally and elongate (Figure 5A, B). The innermost outer lateral tooth bears 7–12 triangular denticles along its inner margin.

The reproductive system (Figure 4B) is triaulic. The pre-ampullary duct is short and narrow. It expands into a thick, saccate ampulla that narrows and passes ventrally under the vas deferens, where it bifurcates into the short oviduct and vas deferens. The proximal part of the vas deferens is prostatic and folded into a large loop. The prostatic vas deferens narrows somewhat as it gives rise to the ejaculatory segment. The vas deferens widens at the

penial sac. The penis exits adjacent to the vaginal duct. The vagina is thin and elongate. It joins the curved, pyriform receptaculum seminis. After a short distance, the vagina and receptaculum join the elongate duct of the bursa copulatrix and the shorter uterine duct. The bursa copulatrix is thin-walled and spherical. The membrane gland is larger than the albumen or mucous glands.

Discussion: The present material is virtually identical to that originally described (Gosliner & Williams, 1975). The only differences are that the bursa copulatrix is spherical in the present material rather than nodular, and there is no vestigial rachidian row of radular teeth. The nodular appearance indicates that the bursa is full of spermatozoa. The previously described vestigial rachidian row is a preservational artifact of the folding of the radular membrane. We reexamined the paratype radula, CASIZ 020376 (formerly 490). No trace of such a row was found in it or any of the present material.

Hallaxa chani is plesiomorphic in all features described, except that the labial rodlets are multifid. It is the only yellowish species with many scattered tubercles.

Hallaxa atrotuberculata

Gosliner & Johnson, sp. nov.

(Figures 1A, 6, 7)

Type material: Holotype: CASIZ 066167, Nosy Komba, Madagascar, 1 m depth, 16 April 1989, T. M. Gosliner. Paratypes: One specimen, BPBM 9943, lagoonside, Enewetak Island (11°21'43"N, 162°21'8"E, Enewetak Atoll, Marshall Islands, 5 m depth, 7 February 1983, S. Johnson. One specimen, BPBM 9944, lagoonside, Enewetak Island, Enewetak Atoll, Marshall Islands, 5 m depth, 7 February 1983, S. Johnson. Two specimens, CASIZ 066168, one dissected, Nosy Tanikely, Madagascar, 2 m depth, 14 April 1989, T. M. Gosliner. One specimen, CASIZ 066169, n.

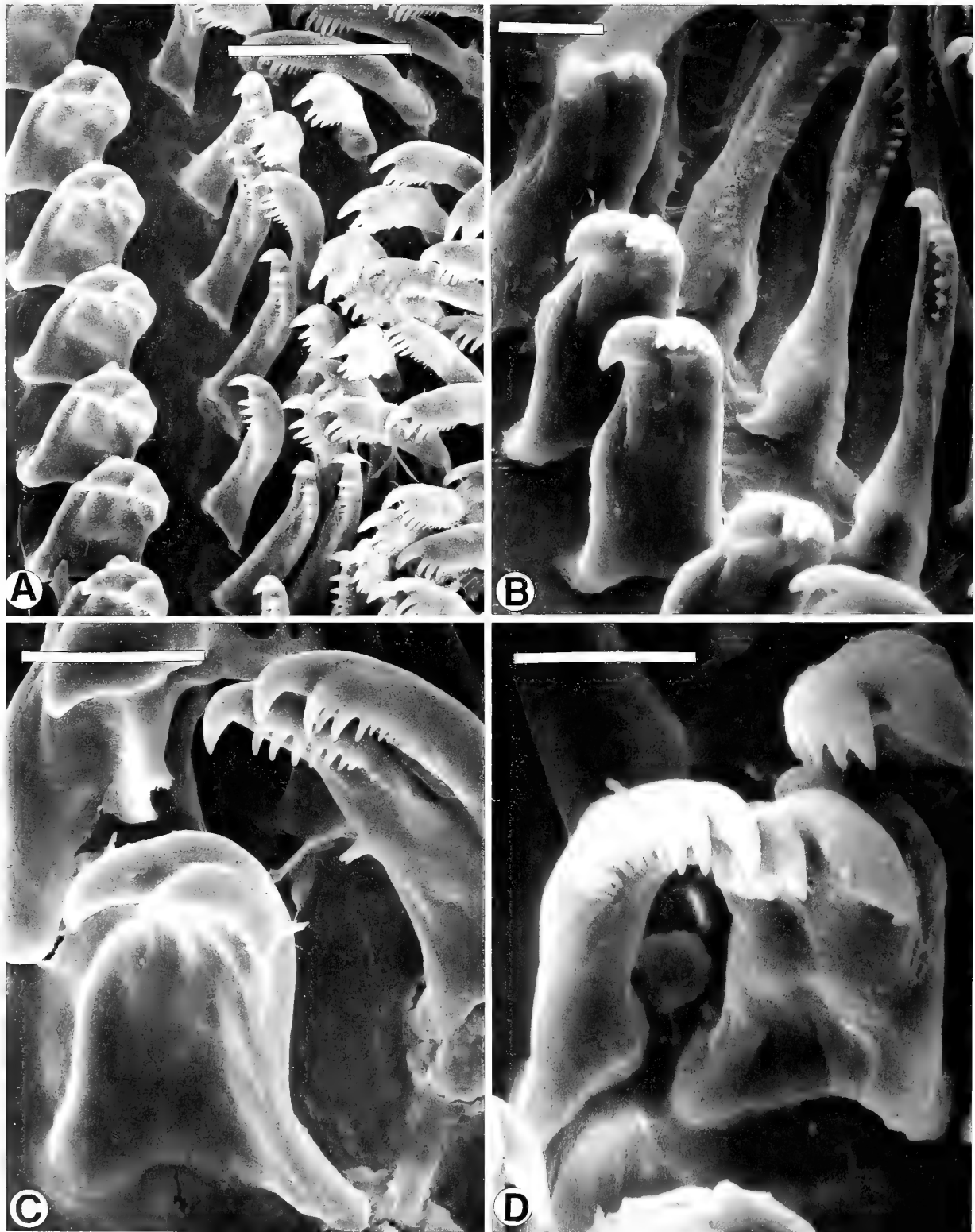


Figure 5

Hallaxa chani Gosliner & Williams, 1975. Scanning electron micrographs of CASIZ 070787. A.-D. Inner and outer lateral teeth, A. scale = 43 μm . B. scale = 20 μm . C. scale = 20 μm . D. scale = 10 μm .

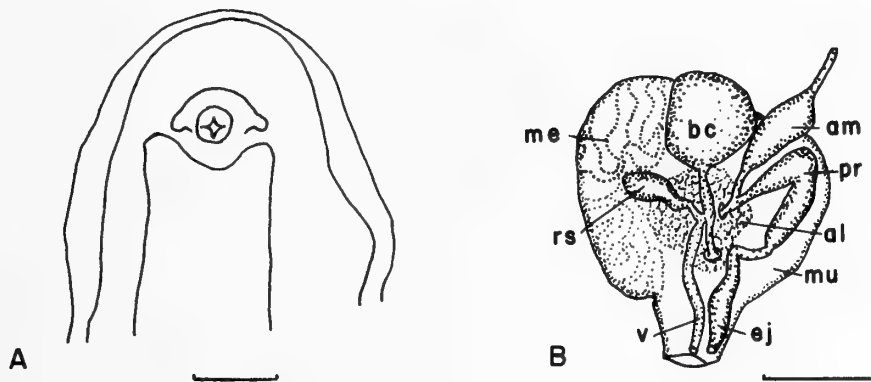


Figure 6

Hallaxa atrotuberculata Gosliner & Johnson, sp. nov. A. Camera lucida line drawing of ventral view of head and foot of preserved specimen, scale = 1.0 mm. B. Reproductive system, al- albumen gland, am- ampulla, bc- bursa copulatrix, ej- ejaculatory portion of vas deferens, me- membrane gland, mu- mucous gland, pr- prostatic portion of vas deferens, rs- receptaculum seminis, v- vagina, scale = 1.0 mm.

side of Andilana Beach, Nosy Be, Madagascar, 15 April 1989, T. M. Gosliner. One specimen, CASIZ 074196, 0.5 km s. of Mahé Beach Hotel, Mahé Island, Republic of the Seychelles, 1 m depth, 2 April 1986.

Distribution: This species has been recorded from the western Indian Ocean from Madagascar and the granitic Seychelles, and from Enewetak Atoll in the western Pacific (present study).

Etymology: The epithet *atrotuberculata* refers to the black tubercles that characterize this species.

External morphology: The living animals (Figure 1A) are 3–18 mm in length. The body is elongate and ovoid. The general body color is light charcoal gray with uniformly scattered black tubercles. The apical portion of the rhinophores is opaque white, while the remainder is black. The gills are uniformly black with an occasional silvery area of pigment located in the center of the plume in the area around the anus of some specimens. The rhinophores are bulbous with 12–14 transverse lamellae. The branchial plume consists of 11–14 unipinnate gills. The anterior end of the foot (Figure 6A) is curved anteriorly, without elongate lateral extensions. A short oral tentacle is present on either side of the mouth.

Internal morphology: The muscular portion of the buccal mass is short relative to the anterior glandular segment. Within the anterior end of the muscular portion of the buccal mass is the labial cuticle. The labial cuticle is composed of several rows of elongate, undivided rodlets (Figure 7A). The radular formula is $27 \times 16.1.0.1.16$, $31 \times 17.1.0.1.17$ (Figure 7B), $33 \times 22.1.0.1.22$ in three specimens examined. The inner lateral teeth are broad and thick with a single primary cusp (Figure 7C, D). On the outer edge of the cusp are one to three small, short denticles. The outer lateral teeth are narrow and elongate (Figure

7E). The innermost outer laterals bear seven to eight elongate denticles. Some of the outer laterals may have as many as 10 denticles along their inner edge. The outermost teeth have only four to five denticles along their margin.

The triaulic reproductive system (Figure 6B) is fully mature. The pre-ampullary duct is narrow and elongate. The ampulla is short and wide. It narrows and divides into the short oviduct and the vas deferens. The vas deferens expands into a folded prostatic portion. The prostatic portion narrows into a thin, curved muscular portion that widens and terminates at the common genital opening. The vaginal opening is immediately adjacent to the distal termination of the vas deferens. The vagina is curved, narrow and elongate. There is a common junction of the vagina with the ducts of the bursa copulatrix and receptaculum seminis, and the uterine duct. The receptaculum seminis is pyriform and elongate. The bursa copulatrix is large and spherical. The female gland mass is composed of three portions—the albumen, membrane, and mucous glands. The membrane gland is not distinctly separated from the albumen and mucous glands.

Discussion: *Hallaxa atrotuberculata* is the only species of *Hallaxa* with large, uniformly scattered tubercles and a black ground color. It also is unique in having an inner lateral tooth with a single broad cusp with minute outer denticles. Also, *H. atrotuberculata* has more outer lateral teeth per half row than any other described species of *Hallaxa*. Its general appearance is reminiscent of species of the closely allied genus *Actinocyclus*. It still retains many primitive features: numerous gills, undivided jaw rodlets, a broad radula, and a thick primary cusp of the inner lateral tooth with secondary denticles. It represents the least derived member of the genus *Hallaxa*. Though it retains some of the primitive features found in species of *Actinocyclus*, it clearly shares several derived features with

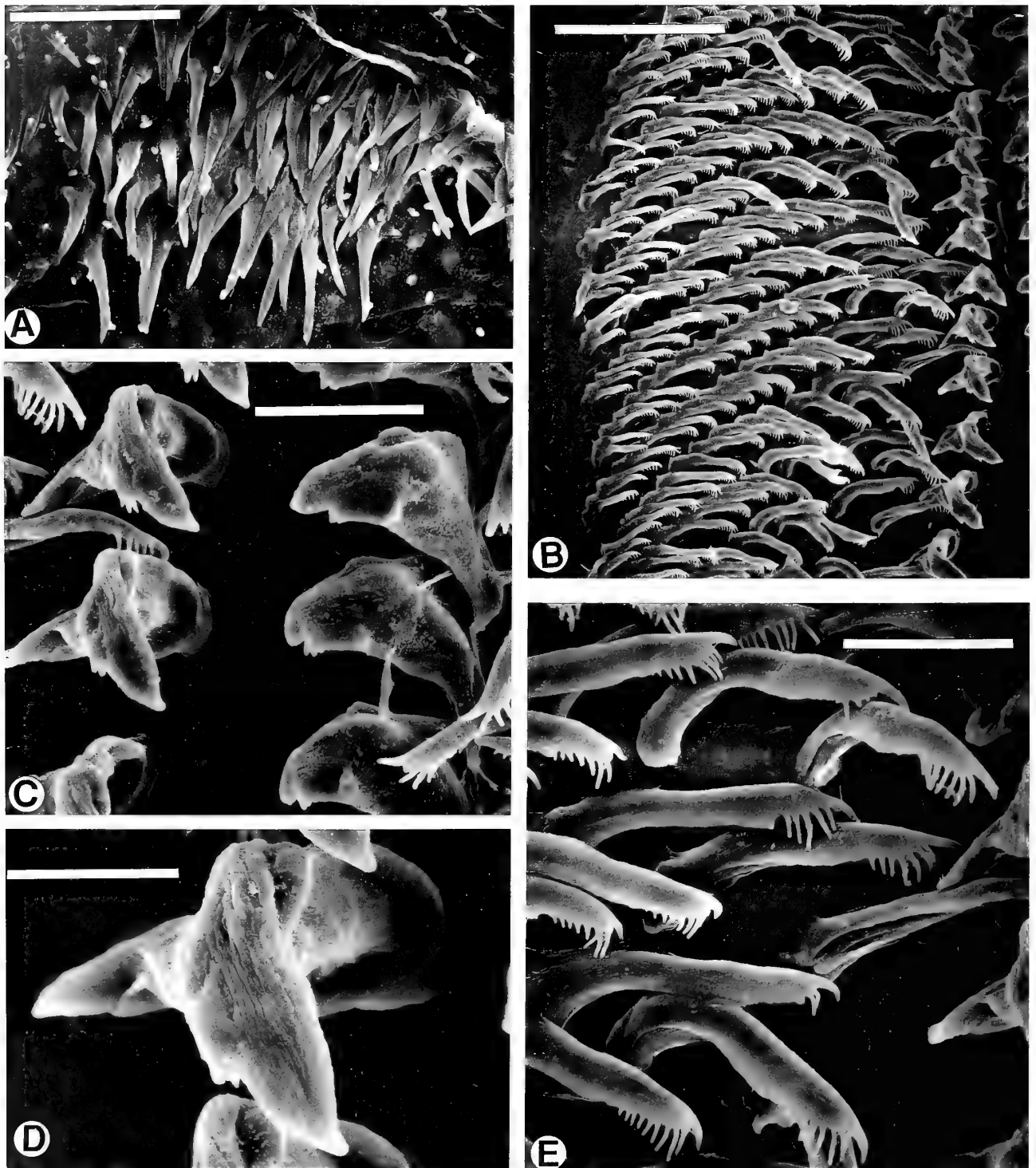


Figure 7

Hallaxa atrotuberculata Gosliner & Johnson, sp. nov. Scanning electron micrographs, CASIZ 066168. A. Jaw rodlets, scale = 20 μm . B. Half row of radular teeth, scale = 100 μm . C. Inner lateral teeth, scale = 30 μm . D. Inner lateral teeth, scale = 15 μm . E. Outer lateral teeth, scale = 30 μm .

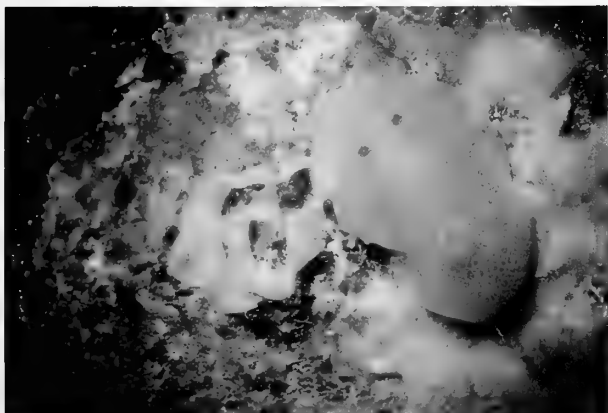


Figure 8

Hallaxa translucens Gosliner & Johnson, sp. nov. Living holotype with egg mass on prey sponge.

other species placed in *Hallaxa* (see systematic relationships).

Hallaxa translucens

Gosliner & Johnson, sp. nov.

(Figures 1B, 8–10)

Type material: Holotype: CASIZ 088079, dissected, 6 m depth, Devil's Point, w. side Maricaban Island, off Luzon Island, Philippines, 23 March 1993, T. M. Gosliner.

Distribution: This species is known only from the holotype collected off the southern coast of Luzon Island in the Philippines.

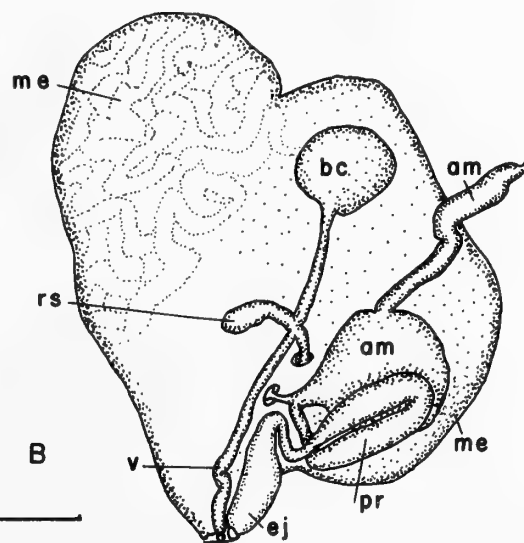
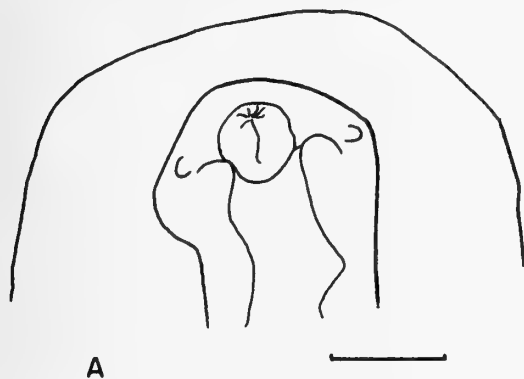


Figure 9

Hallaxa translucens Gosliner & Johnson, sp. nov. A. Camera lucida line drawing of ventral view of head and foot of preserved holotype, scale = 1.0 mm. B. Reproductive system, am- ampulla, bc- bursa copulatrix, ej- ejaculatory portion of vas deferens, me- membrane gland, mu- mucous gland, pr- prostatic portion of vas deferens, rs- receptaculum seminis, v- vagina, scale = 1.0 mm.

Etymology: The name *translucens* comes from the translucent appearance of the living animal.

External morphology: The living animal (Figure 1B, 8) was 20 mm in length. The body is broad and rounded with a smooth notum. The animal is translucent whitish with a dense network of opaque white pigment. The gills are translucent white, and the rhinophores are uniformly light brown.

The branchial plume consists of 12 unipinnate gills. The rhinophores are bulbous with eight simple lamellae. The anterior end of the foot (Figure 9A) is curved and contains anteriorly directed folds. A short, digitiform oral tentacle is present on either side of the mouth.

Internal morphology: The buccal mass is short and muscular, with a short anterior glandular portion. Near the anterior limit of the muscular portion of the buccal mass is the labial cuticle. The cuticle contains numerous rows of undivided and bifid rodlets (Figure 10A). The radular formula of the single specimen is 40 × 13.1.0.1.13 (Figure 10B). The inner lateral teeth (Figure 10C) are relatively narrow basally with a bifid cusp that bears two hook-shaped denticles. No secondary denticles are present on the outer edge of the tooth. The outer lateral teeth (Figure 10D) are thin and elongate. The primary denticle is slightly curved and much longer than the lower denticles. There are 7–11 denticles along the margin of the laterals. The teeth of the innermost outer lateral teeth are more congested and less distinct than those of the outermost teeth. The outermost laterals are as long as the inner ones.

The reproductive system (Figure 9B) is triaulic. The pre-ampullary duct is short and narrow. It expands into

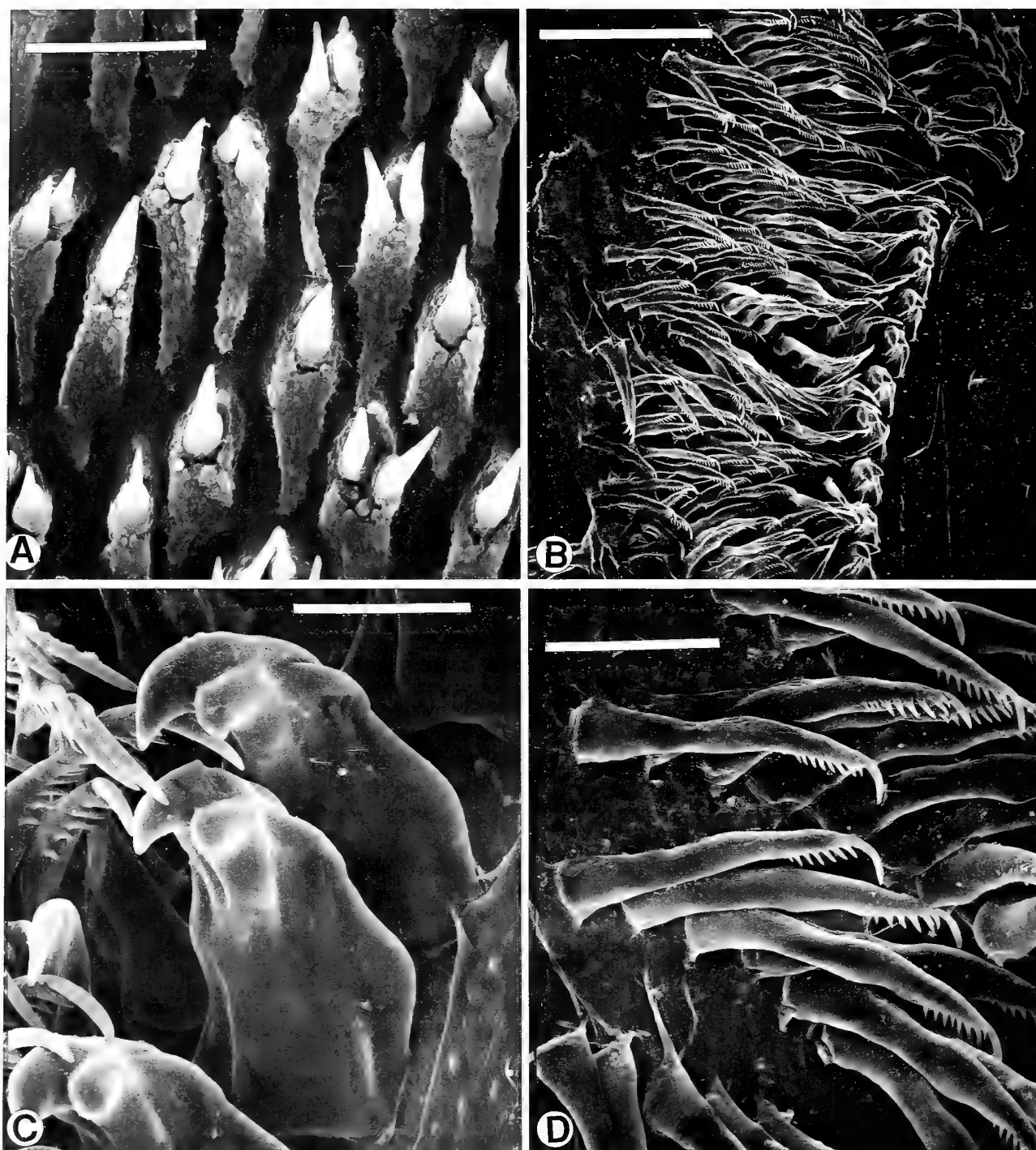


Figure 10

Hallaxa translucens Gosliner & Johnson, sp. nov. Scanning electron micrographs. A. Jaw rodlets of holotype, scale = 10 μm . B. Half row of radular teeth, holotype, scale = 150 μm . C. Inner lateral teeth, holotype, scale = 30 μm . D. Outer lateral teeth, holotype, scale = 43 μm .

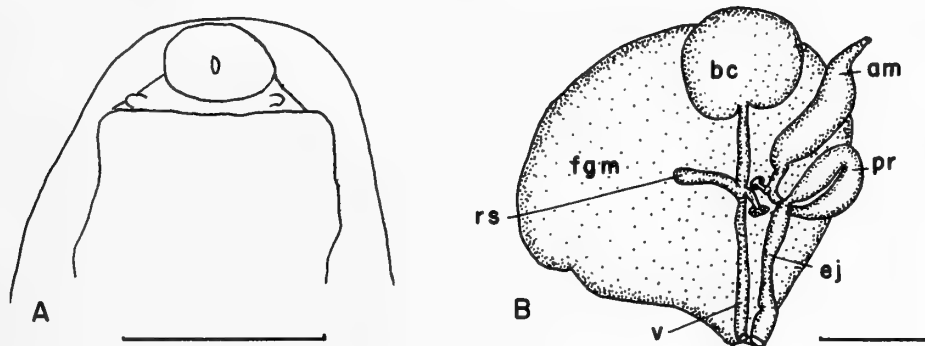


Figure 11

Hallaxa sp. A. Camera lucida line drawing of ventral view of head of preserved specimen, scale = 1.0 mm. B. Reproductive system, am- ampulla, bc- bursa copulatrix, ej- ejaculatory portion of vas deferens, fgm- female gland mass, pr- prostatic portion of vas deferens, rs- receptaculum seminis, v- vagina, scale = 0.5 mm.

a wide, bulbous ampulla. From the ampulla, the narrow, short postampullary duct divides into the short oviduct, which enters the female gland mass, and the vas deferens. The vas deferens expands into a proximal prostatic portion, which recurves back upon itself and narrows into a short segment. From this narrow portion, the duct again widens into a thick ejaculatory penis that is devoid of armature and exits adjacent to the vagina. The vagina is thin and slightly convoluted. The duct of the pyriform receptaculum seminis is short and enters the vagina opposite the uterine duct. The proximal portion of the vagina is thin and elongate and terminates at the stalked, spherical, thin-walled bursa copulatrix. The membrane gland is somewhat separate from the albumen and mucous glands, but not markedly as in some other species.

Discussion: *Hallaxa translucens* externally resembles other species of *Hallaxa* with white body color. It most closely resembles *H. paulinae* and white specimens of *H. cryptica*. There are several differences in the external morphology of these three species. *Hallaxa translucens* has distinct oral tentacles that are absent in *H. cryptica* and *H. paulinae*. *Hallaxa translucens* and *H. paulinae* both are translucent white with an overlying network of opaque white. However, *H. translucens* has brown bulbous rhinophores, while *H. paulinae* has white conical rhinophores with a black subapical spot and few lamellae. Also the opaque white lines are more crowded in *H. translucens*. Internally, there are other differences. In *H. translucens*, the inner lateral tooth lacks the secondary denticles that are present in *H. paulinae*. There are also other differences in the number and shape of the outer lateral teeth. *Hallaxa translucens* has 13 outer lateral teeth per side, while the same-sized specimens of *H. paulinae* have a maximum of six rows of outer laterals. In *H. translucens*, the outer laterals bear 7–11 elongate, crowded denticles. All of the outer lateral teeth are similar in size and shape. In *H. paulinae*, there are zero to seven denticles on the outer lateral teeth. Their denticles are coarser than in *H. translucens*. The outermost

teeth of *H. paulinae* are smaller than the inner outer laterals, and the outermost teeth lack denticles. Also, in *H. translucens*, the vaginal duct between the gonopore and the duct of the receptaculum seminis is elongate, while it is extremely short in *H. paulinae*. The duct of the receptaculum is short in *H. translucens* and elongate in *H. paulinae*.

Hallaxa cryptica lacks the opaque white network of lines present in both *H. translucens* and *H. cryptica*, but has opaque white spots that resemble tubercles. *Hallaxa translucens* has 12 gills compared to eight in *H. cryptica* and has a shorter, curved, and wide ejaculatory portion of the vas deferens.

Hallaxa sp.

(Figures 11, 12)

Material: Two specimens, National Museum of Natural History USNM 577348, Ang Hin Choburi, Thailand, 3 August 1958, George Moore.

External morphology: The two preserved specimens are 7 and 8 mm in length. The body is elongate and ovoid. The branchial plume consists of 11 unipinnate gills. The bulbous rhinophores have six to seven lamellae. The ventral surface of the foot (Figure 11A) is straight, but lacks elongate extensions of the anterior corners. A short tentacle is present on either side of the mouth.

Internal morphology: The buccal mass is short and muscular. At its anterior end is a thin band of undivided jaw rodlets (Figure 12A). There are only three to four rows of rodlets along the region that contains rodlets. The radular formula is $30 \times 6-7.1.0.1.6-7$ in one specimen where the radula is complete. The inner lateral teeth (Figure 12B, C) are only slightly wider than the outer laterals. They have a sharp triangular cusp, with three to four elongate denticles on the outer side of the teeth. The outer lateral teeth (Figure 12D) have four to seven elongate

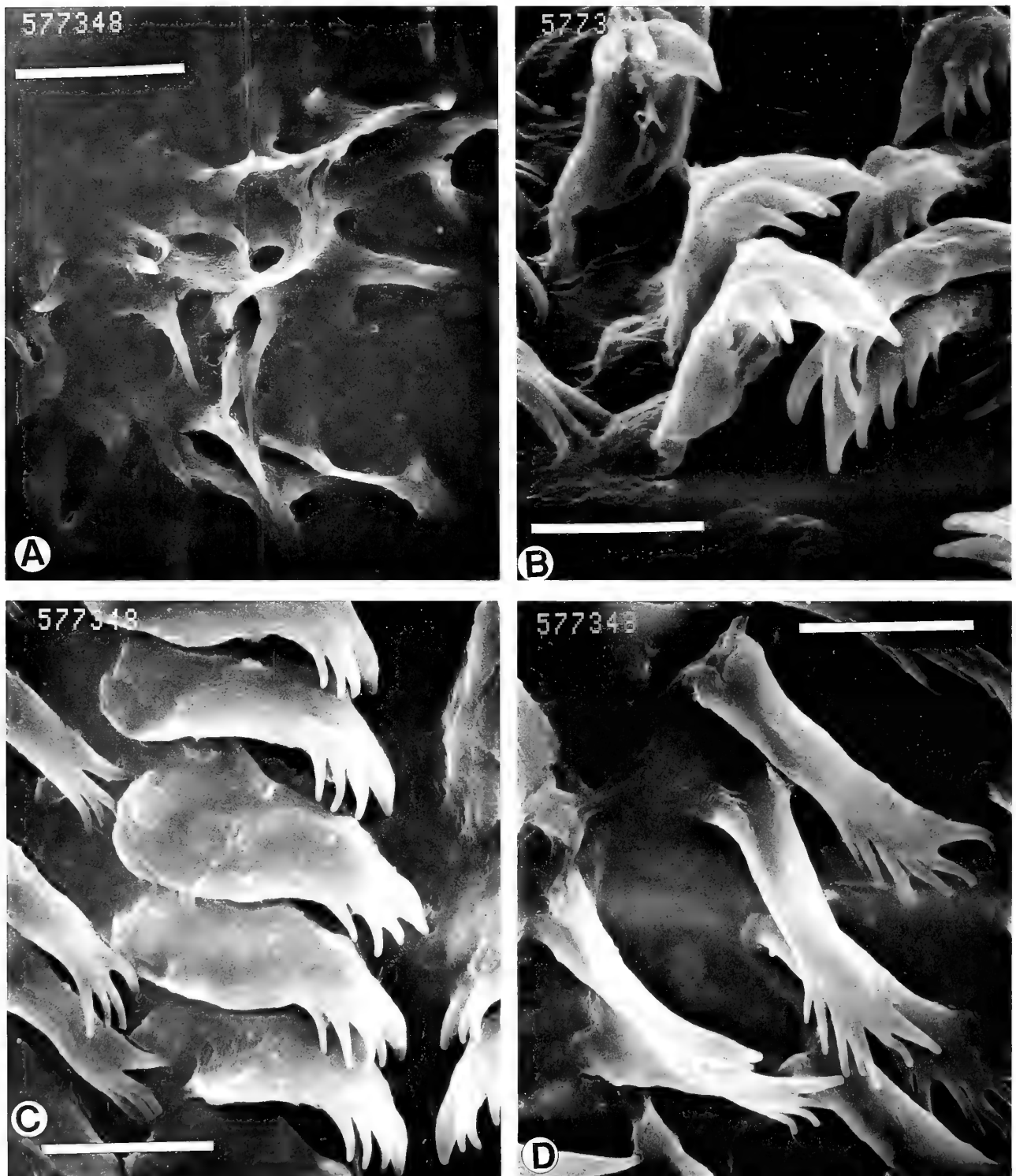


Figure 12

Hallaxa sp. Scanning electron micrographs, USNM 577348. A. Jaw rodlets, scale = 15 μm . B.-C. Inner lateral teeth, B. scale = 7.5 μm , C. scale = 10 μm . D. Outer lateral teeth, scale = 10 μm .

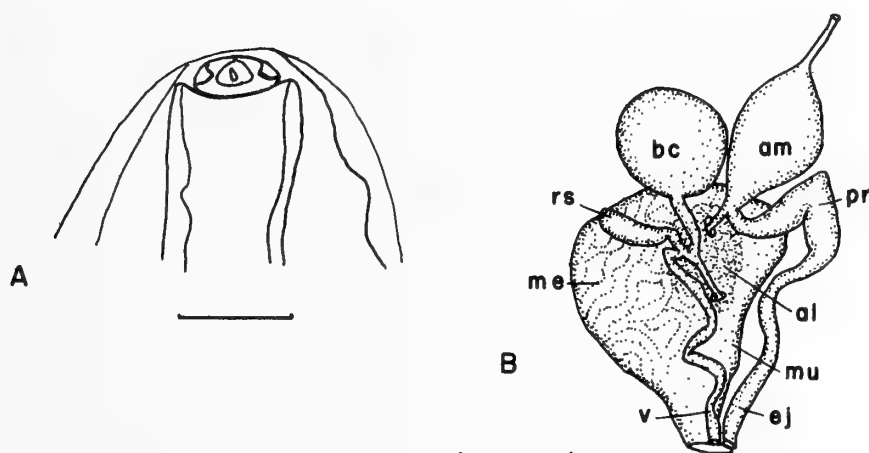


Figure 13

Hallaxa iju Gosliner & Johnson, sp. nov. A. Camera lucida line drawing of ventral view of head of preserved specimen, scale = 1.0 mm. B. Reproductive system, al- albumen gland, am- ampulla, bc- bursa copulatrix, ej- ejaculatory portion of vas deferens, me- membrane gland, mu- mucous gland, pr- prostatic portion of vas deferens, rs- receptaculum seminis, v- vagina, scale = 0.75 mm.

denticles along their surface. Some of the outermost teeth lack denticles entirely.

The reproductive system (Figure 11B) is triaulytic. The pre-ampullary duct is thin and short, and expands into the ampulla. The ampulla again narrows and divides into the short oviduct and the vas deferens. The proximal part of the vas deferens is prostatic. It loops distally and narrows into the ejaculatory portion, which terminates at the common gonopore adjacent to the vagina. The vagina is thin, straight, and elongate. A short, digitiform receptaculum seminis joins the vagina immediately opposite the short uterine duct. The vagina continues proximally, and joins the large, spherical bursa copulatrix. The female gland mass consists of large membrane and mucous glands, and a smaller albumen gland. The membrane gland is continuous with the lobes of the other glands.

Discussion: *Hallaxa* sp. is similar in appearance to *H. decorata*, which is known only from its original, incomplete description. *Hallaxa decorata* differs from the present species in having a stronger cusp on the inner lateral tooth, with more, shorter denticles. It also has more outer lateral teeth per row, and they are more regularly arched in shape, as compared to the more fimbriate denticulation of the present material. The present material has radular teeth that are similar in form to *H. gilva*, but again has fewer teeth per half row. It also differs from *H. gilva*, and all other species of *Hallaxa*, in having a reduced area of jaw rodlets. The labial rodlets of *H. sp.* are undivided rather than multifid, as in *H. gilva*. Most other species have at least 10 rows of rodlets. It would appear that the present material represents an undescribed species. Since the appearance of the living animal remains unknown, we have decided not to describe this species at present.

Hallaxa iju Gosliner & Johnson, sp. nov.

(Figures 1C, 13, 14)

Type material: Holotype, California Academy of Sciences, CASIZ 069937, Barracuda Point, e. side of Pig Island, Madang Lagoon, Madang Province, Papua New Guinea, 9 m depth, 27 August 1989, E. Sobeck. Paratypes: One specimen, BPBM 9945, under dead coral, Reefer 8 Pinnacle, Enewetak Atoll, Marshall Islands, 15 m depth, 6 September 1981, S. Johnson. One specimen, BPBM 9946, lagoonside, Enewetak Island, Enewetak Atoll, Marshall Islands, under dead coral head, 3 m depth, 19 September 1981, S. Johnson. One specimen, CASIZ 079271, dissected, Horseshoe Cliffs, 1 km wnw. of Onna Village, Okinawa, Ryukyu Islands, 3 m depth, 18 July 1991, R. F. Bolland. One specimen, CASIZ 075835, outer barrier reef, s. of Wongat Island, Madang Lagoon, Papua New Guinea, 24 November 1990, T. M. Gosliner. One specimen, CASIZ 083755, Layaglayag, n. side of Maricaban Island, off s. end of Luzon Island, Philippine Islands, 9 m depth, 24 February 1992, T. M. Gosliner.

Distribution: This species has been found at several localities in the western Pacific, from the Marshall Islands, Papua New Guinea, Okinawa, and the Philippines.

Etymology: The specific name is the Marshallese word for star, which refers to the stellate appearance of the rhinophores when viewed from above.

External morphology: The living animals (Figure 1C) are 6–8 mm in length. The body is elongate, ovoid, largely reddish-brown to black. There are small, scattered opaque white spots situated on small tubercles scattered on the notum and on the basal third of the gills. Opaque white

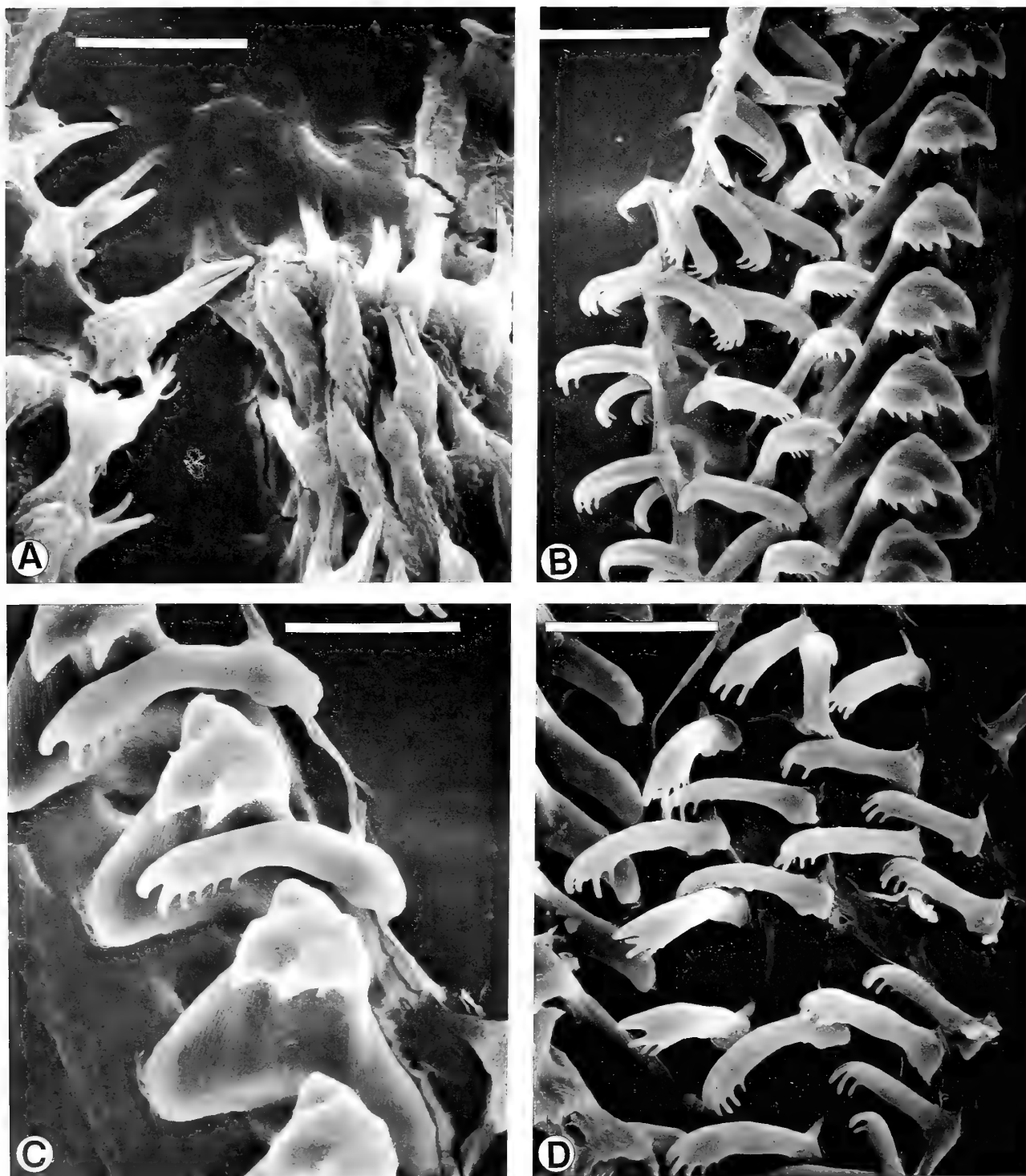


Figure 14

Hallaxa iju Gosliner & Johnson, sp. nov. Scanning electron micrographs. A. Jaw rodlets, Okinawa, CASIZ 079271, scale = 7.5 μm. B. Half row of radular teeth, Okinawa, CASIZ 079271, scale = 30 μm. C. Inner lateral teeth, Enewetak, BPBM 9945, scale = 15 μm. D. Outer lateral teeth, Philippines, CASIZ 083755, scale = 20 μm.

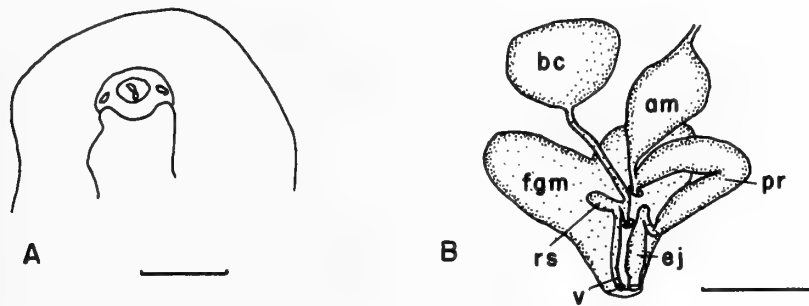


Figure 15

Hallaxa elongata Gosliner & Johnson, sp. nov. A. Camera lucida line drawing of ventral view of head, scale = 1.0 mm. B. Reproductive system, am- ampulla, bc- bursa copulatrix, ej- ejaculatory portion of vas deferens, fgm- female gland mass, pr- prostatic portion of vas deferens, rs- receptaculum seminis, v- vagina, scale = 0.75 mm.

pigment covers the distal two-thirds of the rhinophoral rachis and lamellae in most specimens. There are five to nine expanded rhinophoral lamellae. The branchial plume consists of 8–10 unipinnate gills. The foot (Figure 13A) is somewhat curved anteriorly, but is straighter than that of most other species. A short, triangular oral tentacle is present on either side of the mouth.

Internal morphology: The buccal mass is short and muscular posteriorly, and elongate and glandular anteriorly. At the anterior end of the muscular portion of the buccal mass is the thin labial cuticle, which bears several rows of rodlets. The rodlets (Figure 14A) are undivided, bifid, or trifold. The radular formula is $14 \times 4.1.0.1.4$, $19 \times 6.1.0.1.6$, $20 \times 8.1.0.1.8$, $22 \times 5.1.0.1.5$ and $26 \times 10.1.0.1.10$ in five specimens examined. The inner lateral teeth (Figure 14B, C) are broad and thick. The free margin bears a bifid cusp with two primary denticles. The outer cusp may have a series of zero to three denticles on the outer side of the cusp. The only specimen that lacked denticles on some teeth was the smallest specimen examined. Some of the inner lateral teeth have one or two denticles on the margin, while others in the same specimen lack denticles entirely (Figure 14C). The outer lateral teeth are narrow basally and elongate. They bear a series of sparse denticles on their inner margin. The innermost outer lateral teeth (Figure 14C) have 4–12 denticles, while the outermost teeth (Figure 14D) have three to five denticles.

The reproductive system (Figure 13B) is triaulic. The pre-ampullary duct is narrow and short. The ampulla is straight and inflated. It narrows and divides into a short oviduct and vas deferens. The vas deferens expands into a folded prostatic portion. The prostatic portion narrows into a muscular portion that is the same diameter through most of its length. It terminates at the common genital opening. The vaginal opening is immediately adjacent to the proximal termination of the vas deferens. The vagina is narrow and elongate. It includes several loops and joins the ducts of the receptaculum seminis. After a short distance, these combined ducts join with the duct of the bursa copulatrix and the uterine duct. The receptaculum seminis

is pyriform and elongate. The bursa copulatrix is large and spherical. The female gland mass is composed of three portions, the albumen, membrane, and mucous glands, which are not well-separated from each other.

Discussion: *Hallaxa iju* can be immediately distinguished from all other members of the genus by the expanded margins of the rhinophoral lamellae. The radula, with multiple denticles along the margin of the inner lateral tooth, is similar to that described for six other species of *Hallaxa*. Of these, only *H. atrotuberculata* and *H. iju* are darkly pigmented. In contrast to *H. atrotuberculata*, *H. iju* lacks distinct tubercles and has a smooth notum and a much narrower radula.

Hallaxa elongata Gosliner & Johnson, sp. nov.

(Figures 1D, 15, 16)

Type material: Holotype: CASIZ 074119, between Passe Femme and Passe du Bois, Aldabra Atoll, Republic of the Seychelles, intertidal, 21 March 1986, B. F. Kensley. Paratypes: Two specimens, California Academy of Sciences, CASIZ 074153, between Passe Femme and Passe du Bois, Aldabra Atoll, in coral rubble, intertidal, 21 March 1986, T. M. Gosliner. One specimen, CASIZ 074259, between Passe Femme and Passe du Bois, Aldabra Atoll, intertidal, 21 March 1986, B. F. Kensley. Four specimens, CASIZ 074249, two dissected, same locality as above, intertidal 19 March 1986, T. M. Gosliner. One specimen, CASIZ 074162, same locality and date as above. Two specimens, CASIZ 074256, same locality and date as above.

Distribution: This species is presently known only from Aldabra Atoll, in the western Indian Ocean, where it is found intertidally in coralline algal rubble.

Etymology: The specific name *elongata* comes from the relatively thin, elongate body, when compared to other members of the genus.

External morphology: The living animals (Figure 1C) are 5–12 mm in length and elongate, elliptical in shape.

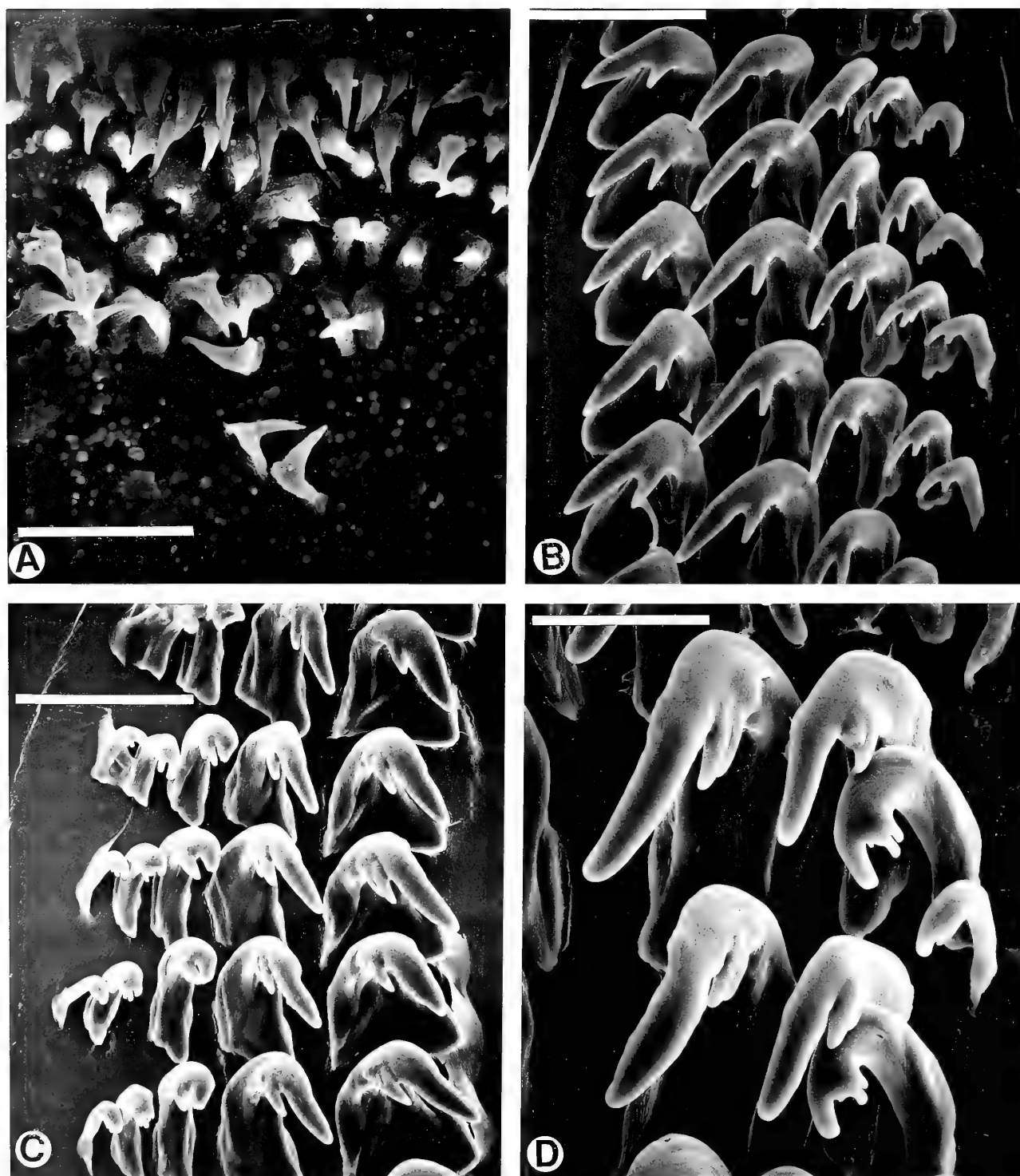


Figure 16

Hallaxa elongata Gosliner & Johnson, sp. nov. CASIZ 074249. A. Jaw rodlets, scale = 25 μ m. B. Half row of radular teeth, scale = 43 μ m. C. Half row of radular teeth, scale = 60 μ m. D. Outer lateral teeth, scale = 25 μ m.

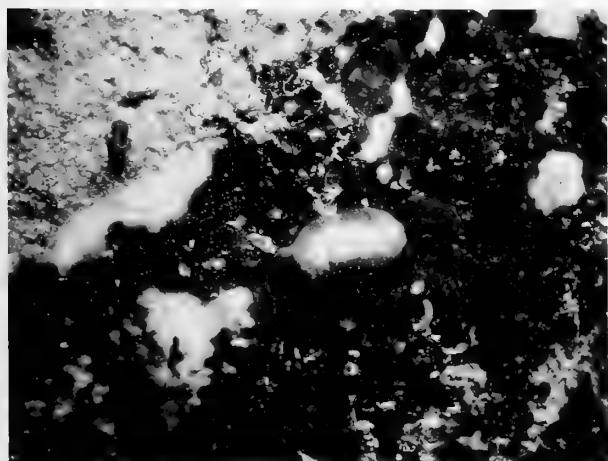


Figure 17

Hallaxa albopunctata Gosliner & Johnson, sp. nov. Living animal.

The animal is uniformly lime green in color with scattered opaque white spots on the tips of minute, scattered tubercles. The apical third of the rhinophores is covered with opaque white, while the basal two-thirds is green. The gills are covered with opaque white pigment. The branchial plume is composed of seven to nine unipinnate gills. The rhinophores are bulbous with seven to nine lamellae. The anterolateral margins of the foot (Figure 15A) are anteriorly directed, and the foot is curved. On either side of the mouth is a folded depression, but no oral tentacles are present.

Internal morphology: The buccal mass is muscular posteriorly, with a larger anterior glandular portion. At the anterior end of the muscular portion of the buccal mass is the labial cuticle. The cuticle contains several rows of largely simple, undivided rodlets (Figure 16A), though an occasional bifid rodlet may be present. The radular formula is $25 \times 4.1.0.1.4$ in the two specimens examined. The inner lateral teeth (Figure 16B, C) are broad and thick. They bear an elongate cusp on their inner side. On the outer side are one to two smaller denticles. The succeeding lateral teeth (Figure 16D) are successively narrower, but not as markedly as in other species. The second through fifth laterals also have one or two laterals on the outside of the primary cusp.

The reproductive system (Figure 15B) is triaulic and largely mature in the largest specimen. The pre-ampullary duct is short and expands into a wide, saccate ampulla. The ampulla narrows abruptly and divides into the short oviduct and the vas deferens. The proximal portion of the vas deferens is prostatic and folded. The prostatic portion narrows into a short, straight ejaculatory segment that is highly muscularized. The vas deferens terminates adjacent to the vaginal duct. The vagina is extremely thin and flimsy. This may reflect that, even in the largest specimens

collected, the female reproductive system may not be fully mature. The vagina is straight and joins the duct of the digitiform receptaculum seminis immediately prior to their common junction with the uterine and bursa copulatrix ducts. The bursa is large and spherical with a thin, elongate duct.

Discussion: This species is distinguishable from other members of the genus by its elongate body form. Internally, it differs from other species of *Hallaxa* by its distinctive radular morphology. It is the only species in which the first outer lateral tooth does not differ markedly from the innermost lateral. The outermost teeth are more similar to those found in other members of the genus, but have fewer denticles than other species. There is little doubt that this species is closely allied to other species of *Hallaxa*, despite the radular differences. It shares similar derived reproductive morphology and the unique arrangement of the oral region and foot, complete with glandular pits.

Hallaxa albopunctata Gosliner & Johnson, sp. nov.

(Figure 17–19)

Hallaxa sp. Gosliner, 1987:69, fig. 91.

Type material: Holotype, SAM A35367, radula removed, Vetchies Pier, n. of Durban Harbor, Durban, South Africa, 2 m depth, 28 April 1982, T. M. Gosliner. Paratype, dissected, SAM A38164, same locality and date as holotype.

Distribution: This species has been collected only from the type locality, Durban, Natal, South Africa.

Etymology: The name *albopunctata* refers to the small white punctations found on the notum of this species.

External morphology: The living animals (Figure 17) are 6 mm in length. The general body color is pale translucent yellow. The body is elongate and ovoid in shape. Scattered opaque white spots are present on low, irregular tubercles distributed unevenly around the notum. Brownish pigment is present around the base of the rhinophore club. The rhinophores are bulbous with seven simple lamellae in the two specimens. The branchial plume consists of seven to eight unipinnate gills. The foot (Figure 18A) is curved anteriorly. The anterior foot corners are elongate and anteriorly directed. A small pit is present on either side of the mouth.

Internal morphology: The labial cuticle consists of numerous multifid rodlets. The radular formula is $24 \times 7.1.0.1.7$ in the one specimen with the complete radula. The inner lateral teeth are broad and thick (Figure 19A–C). They bear a single primary cusp on their inner side and three to four smaller denticles on the outer side. The outer lateral teeth are narrow basally, and elongate; and bear five to seven elongate denticles along their inner margin (Figure 19A, B, D).

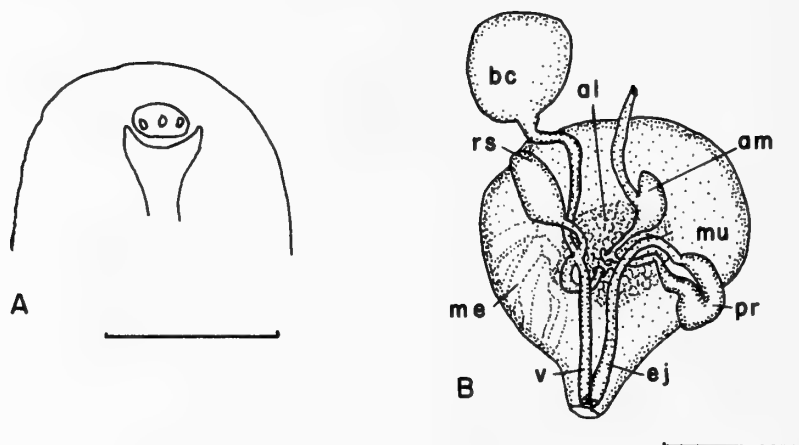


Figure 18

Hallaxa albopunctata Gosliner & Johnson, sp. nov. A. Camera lucida line drawing of ventral view of head and foot of preserved specimen, scale = 1.0 mm. B. Reproductive system, al- albumen gland, am- ampulla, bc- bursa copulatrix, ej- ejaculatory portion of vas deferens, me- membrane gland, mu- mucous gland, pr- prostatic portion of vas deferens, rs- receptaculum seminis, v- vagina, scale = 0.5 mm.

The reproductive system (Figure 18C) is triauleic. The pre-ampullary duct is elongate and thin. It widens into a short, saccate ampulla. The ampulla narrows and bifurcates into the vas deferens and the oviduct. The vas deferens widens into a curved prostatic portion. The duct is constricted in the region where the prostatic portion ends and the ejaculatory portion begins. The ejaculatory portion is elongate and terminates in the penis adjacent to the thin vaginal duct. The vagina is thin and elongate throughout its length. The bursa copulatrix is thin and spherical with a thin, elongate duct. The receptaculum seminis is thick and pyriform, with a short duct. The ducts of the bursa and receptaculum join the vagina in a common junction with the short uterine duct. The mucous gland is much larger than the membrane or albumen glands.

Discussion: *Hallaxa albopunctata* is similar to *H. elongata* and *H. gilva* Miller, 1987, in having a yellowish to greenish body color. However, *H. albopunctata* is unique in having a broad, multicuspid inner lateral tooth. *Hallaxa albopunctata* and *H. elongata* have an oral pit on either side of the mouth, while *H. gilva* retains oral tentacles. *Hallaxa albopunctata* has outer lateral teeth similar to those found in other members of the genus, while those of *H. elongata* are highly modified and more similar to the inner lateral teeth.

Hallaxa paulinae Gosliner & Johnson, sp. nov.

(Figures 1E, 20, 21)

Type material: Holotype, CASIZ 070401, Manado, Sulawesi, Indonesia, 5 m depth, 24 May 1989, P. Fiene-Severns. Paratype, dissected, CASIZ 069938, same locality and date as holotype. This species was found on an unidentified white sponge, on which it was cryptic.

Distribution: This species is thus far known from Indonesia.

Etymology: This species is named for Pauline Fiene-Severns, who found the type material of this species.

External morphology: The preserved specimens were 15 and 20 mm in length. The living animals (Figure 1E) are round in outline, translucent white with numerous, irregular patches forming a network of opaque white on the smooth notum. The gills are uniformly white. The rhinophores are white with a black subapical spot. The smaller specimen (paratype) has a branchial plume consisting of nine unipinnate gills, while the holotype has eight gills. The rhinophores (Figure 20A) are small and conical in shape. They have only four to five lamellae. The foot (Figure 20B) is curved anteriorly. The anterior foot corners are triangular and anteriorly directed. A small pit is present on either side of the mouth in both specimens.

Internal morphology: The muscular portion of the buccal mass is short, while the more anterior, glandular portion is elongate. Within the anterior portion of the muscular portion is the labial cuticle, which contains several rows of rodlets. The rodlets (Figure 21A) consist of one to five denticles along the outer margin. The radular formula is $29 \times 6.1.0.1.6$ in the paratype specimen. The inner lateral teeth (Figure 21B, C) are broad, but somewhat thinner than those of other species examined. The free end of the tooth bears two curved cusps, with one to three auxiliary denticles at the base of the outer cusp. The six outer lateral teeth per half row are narrow and elongate (Figure 21D). The innermost of the outer laterals bear five to seven well-spaced triangular denticles along their inner margin. The succeeding outer laterals have fewer or more reduced denticles. The outermost laterals lack denticles entirely.

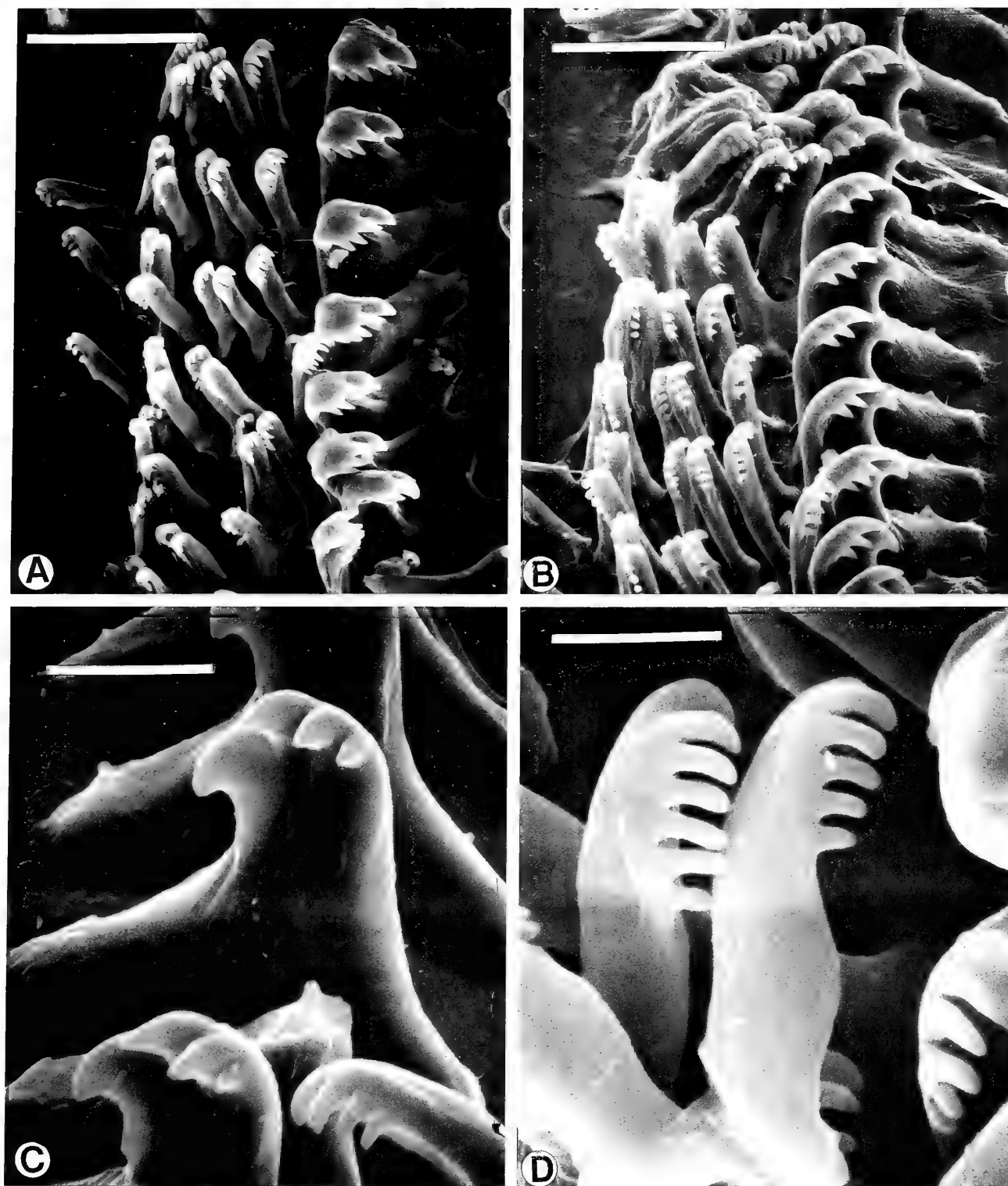


Figure 19

Hallaxa albopunctata Gosliner & Johnson, sp. nov. Scanning electron micrographs, SAM A35367. A. Half row of radular teeth, scale = 30 µm. B. Half row of radular teeth, = 30 µm. C. Half row of radular teeth, scale = 10 µm. D. Outer lateral teeth, scale = 6 µm.

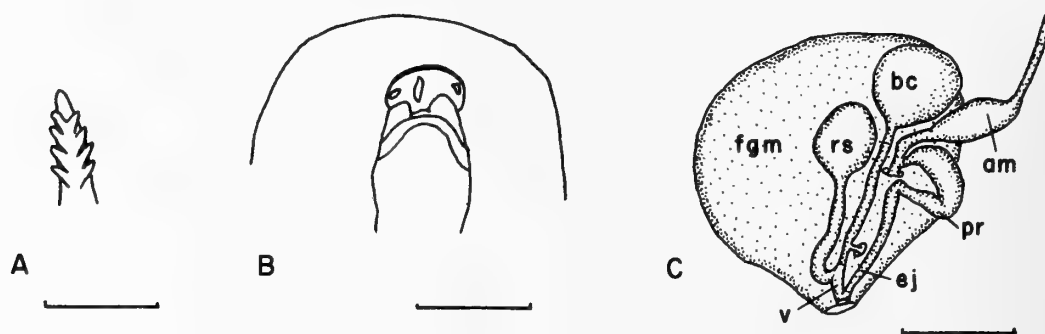


Figure 20

Hallaxa paulinae Gosliner & Johnson, sp. nov. A. Rhinophore, scale = 2.0 mm. B. Camera lucida line drawing of ventral view of head and foot of preserved specimen, scale = 2.0 mm. C. Reproductive system, am- ampulla, bc- bursa copulatrix, ej- ejaculatory portion of vas deferens, fgm- female gland mass, pr- prostatic portion of vas deferens, rs- receptaculum seminis, v- vagina, scale = 1.0 mm.

The reproductive system (Figure 20C) is triaulic. The pre-ampullary duct is thin and elongate. It expands into the short, saccate ampulla. The ampulla narrows and divides into the short oviduct and the vas deferens. The proximal portion of the vas deferens is prostatic and curved. More distally, the vas deferens narrows into the straight, muscular ejaculatory portion, which terminates at the male gonopore. The distal portion of the vagina is exceedingly short and joins the elongate, curved duct of the relatively large, pyriform receptaculum seminis. After a short distance, these ducts join the short uterine duct and the thin, elongate duct of the bursa copulatrix. The bursa is large and spherical. The glands composing the female gland mass were not well-differentiated in the dissected paratype.

Discussion: Only three species of *Hallaxa* have a whitish body color, *H. paulinae*, *H. translucens*, and the white form of *H. cryptica*; and all of these have a broad foot and are cryptic on sponges. *Hallaxa paulinae* and *H. translucens* have a reticulate pattern on the notum, while *H. cryptica* has large white spots that appear to be tubercles, but are not elevated from the notum. *Hallaxa translucens* and *H. cryptica* also have bidenticulate radular teeth with no auxiliary denticles, while *H. paulinae* has one to three denticles along its outer margin. *Hallaxa paulinae* also has fewer, more sparsely spaced denticles (five to seven) on the outer lateral teeth than do either *H. translucens* (7–11) or *H. cryptica* (7–12). *Hallaxa paulinae* is also unique in having small, conical rhinophores and a short distal vaginal duct.

Hallaxa indecora (Bergh, 1905)

(Figures 22, 23)

Halla indecora Bergh, 1905:116, pl. 15, figs. 3–6.

Hallaxa indecora Bergh, Eliot, 1909:90 (*Halla* Bergh, 1878, preoccupied by *Halla* A. Costa, 1844, a genus of polychaete annelids); Vayssière, 1912:33, pl. 1, figs. 11–12, pl. 5, figs. 64–70; Baba, 1949:61, fig. 73, pl. 23, fig. 82.

Hallaxa decorata O'Donoghue, 1929:814, fig. 224 (not Bergh, 1878).

Noumea violacea Risbec, 1930:281, figs. 23–30, pl. 1, fig. 5, syn. nov.

Material: One specimen, CASIZ 079357, Horseshoe Cliffs, 1 km wnw. of Onna Village, Okinawa, 3 m depth, 30 May 1991, R. F. Bolland. One specimen, CASIZ 084863, 100 m w. of Waiki-zaki, 5 m depth, 23 July 1991, R. F. Bolland. One specimen, CASIZ 079366, Horseshoe Cliffs, 1 km wnw. Onna Village, Okinawa, Ryukyu Islands, 3 m depth, 23 July 1991, R. F. Bolland.

Distribution: This species is known from Indonesia (Bergh, 1905), the Gulf of Aden (Vayssière, 1912), Gulf of Suez (O'Donoghue, 1929), New Caledonia (Risbec, 1930), Japan (Baba, 1949), and Okinawa (present study).

External morphology: The living animal is light plum in appearance. Upon closer examination, the notum is translucent white with minute, scattered maroon spots. The body is elongate and ovoid with a smooth notum. The rhinophores and gills are uniformly purplish-brown. The rhinophores are bulbous with seven lamellae. The branchial plume consists of seven unipinnate gills. The foot (Figure 22A) is curved anteriorly, and the anterior foot corners are thin and anteriorly directed. A pit is present on either side of the mouth.

Internal morphology: The buccal mass is short and muscular. The anterior portion is surrounded by a mass of oral glands. Inside the anterior end of the muscular portion of the mass is a circular ring of labial armature. The armature (Figure 23A) consists of a series of rows of irregular rodlets. The radular formula, in the single specimen examined, is $24 \times 8.1.0.1.8$. the inner lateral teeth (Figure 23B, C) are broad and thick. They are curved apically and terminate with a pair of hook-shaped denticles. The two cusps lack any secondary denticles. The outer lateral teeth (Figure 23B, C) are all narrow and elongate,

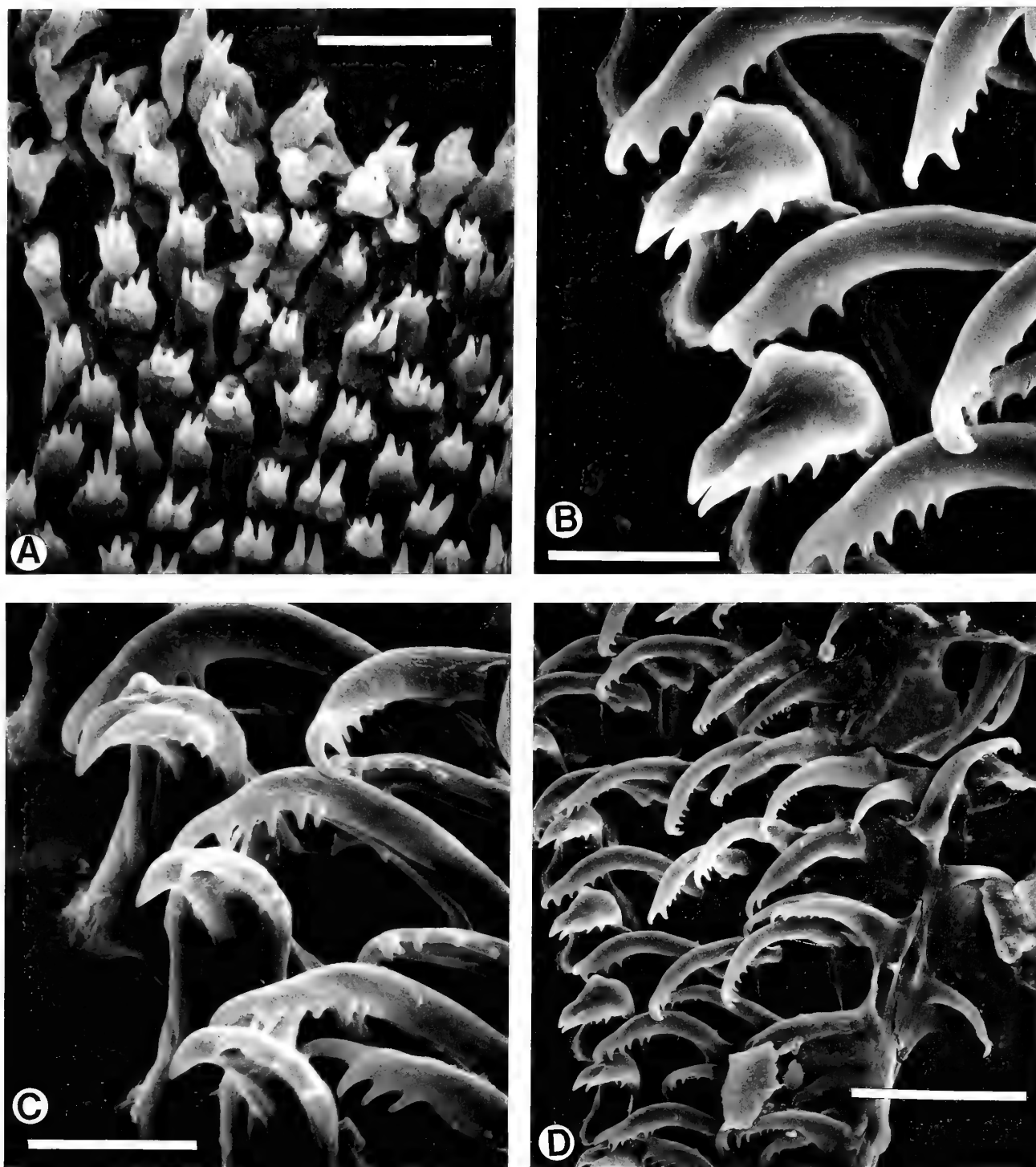


Figure 21

Hallaxa paulinae Gosliner & Johnson, sp. nov., CASIZ 070401. A. Jaw rodlets, scale = 15 μm . B. Inner lateral teeth, scale = 15 μm . C. Inner lateral teeth, scale = 15 μm . D. Outer lateral teeth, scale = 43 μm .

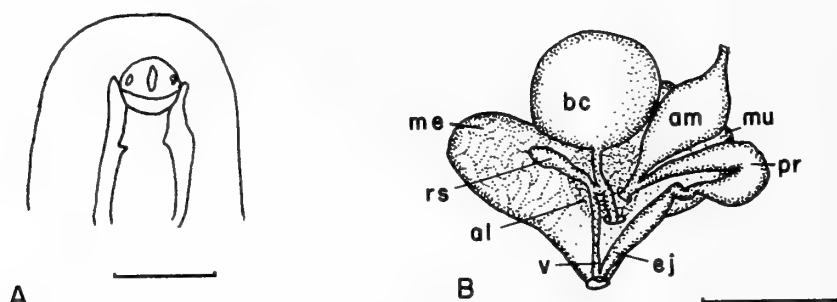


Figure 22

Hallaxa indecora (Bergh, 1905). A. Camera lucida line drawing of ventral view of head and foot of preserved specimen, scale = 0.5 mm. B. Reproductive system, al- albumen gland, am- ampulla, bc- bursa copulatrix, ej- ejaculatory portion of vas deferens, me- membrane gland, mu- mucous gland, pr- prostatic portion of vas deferens, rs- receptaculum seminis, v- vagina, scale = 0.25 mm.

with a series of 12–15 triangular denticles along their inner margin. All of the outer laterals are of similar size and dentition.

The reproductive system (Figure 22B) is triaulic. The narrow pre-ampullary duct expands into a straight, wide ampulla. The ampulla again narrows and divides into the short oviduct and the vas deferens. The proximal part of the vas deferens is wide and prostatic. It curves more distally and narrows into the ejaculatory segment, which terminates at the male gonopore. The vagina is narrow and straight. After a moderate distance, it joins the digitiform receptaculum seminis. After a short distance, the receptaculum duct joins the duct of the bursa copulatrix and the uterine duct. The large bursa is stalked, thin-walled, and spherical. The female gland mass consists of the albumen, membrane, and mucous glands. The membrane gland consists of a discrete lobe largely separate from the other two glands.

Discussion: *Hallaxa indecora* was originally described from nine specimens collected from Aru Island, Indonesia (Bergh, 1905). The radular formula of one specimen described as $60-65 \times 15-20.1.0.1.15-20$. Subsequently, Vayssi re (1912), O'Donoghue (1929, as *H. decorata*), and Baba (1949) recorded specimens from the Gulf of Aden, the Gulf of Suez and Japan. These specimens had radular formulae of $25 \times 6.1.0.1.6$, $33 \times 7.1.0.1.7$, $18-20 \times 8.1.0.1.8$, respectively. The present material from Okinawa is identical in external appearance to that described by Vayssi re, O'Donoghue, and Baba. It agrees in radular formula and shape of teeth. No species of *Hallaxa*, other than Bergh's original description of *H. indecora*, has been described with more than 40 rows of radular teeth (Gosliner & Williams, 1975; Miller, 1987; present study). It is likely that Bergh's count of the radular formula was in error, though the possibility that the material studied by Baba and here may represent a distinct species cannot be eliminated.

Risbec (1930) described *Noumea violacea* based on four specimens collected from New Caledonia. This species is

clearly a *Hallaxa*, based on its bifid inner lateral tooth and elongate, denticulate outer laterals. The color was uniformly wine red in color. It had a radular formula of $20 \times 8.1.0.1.8$. The outer lateral teeth had up to 17 denticles on their margin. All of these features are consistent with the anatomy described for *H. indecora*. On this basis, *Noumea violacea* is here regarded as a junior synonym of *Hallaxa indecora*.

Hallaxa indecora is closely allied to the four other species that have an inner lateral tooth with two large cusps and lack small, auxiliary denticles. The only other species with a purplish color are *H. hileenae* and the purple form of *H. cryptica*. *Hallaxa hileenae* is distinguished from *H. indecora* by having black maculations and a distinct y-shaped ridge on the notum. *Hallaxa indecora* also has more, finer denticles on the outer lateral teeth than does *H. hileenae*. *Hallaxa cryptica* differs in details of coloration, morphology of the anterior foot corners, labial armature, and outer lateral radular tooth denticulation.

Hallaxa hileenae Gosliner & Johnson, sp. nov.

(Figures 1F, 24, 25)

Type material: Holotype, CASIZ 075826, outer barrier reef, between Sek Passage and Wongat Island, Madang Lagoon, Madang, Papua New Guinea, 17 m depth, 25 November 1990, M. Jebb. Paratypes, two specimens partially dissected, CASIZ 086402, s. side Rasch Passage, Madang Lagoon, Madang Province, Papua New Guinea, 6 m depth, 16 June 1992, T. M. Gosliner. Paratype, one specimen, (CASIZ 085971) s. side of lighthouse, 3 km n. of Dakak Resort, near Dapitan City, northern Zamboanga, Mindinao, Philippines, 7 m depth, 31 March 1993, T. M. Gosliner.

Distribution: This species is known from Papua New Guinea, the Philippine Islands, and Guam (Clay Carlson and Patty Jo Hoff, personal communication).

Etymology: This species is named for Eileen Sobeck, who

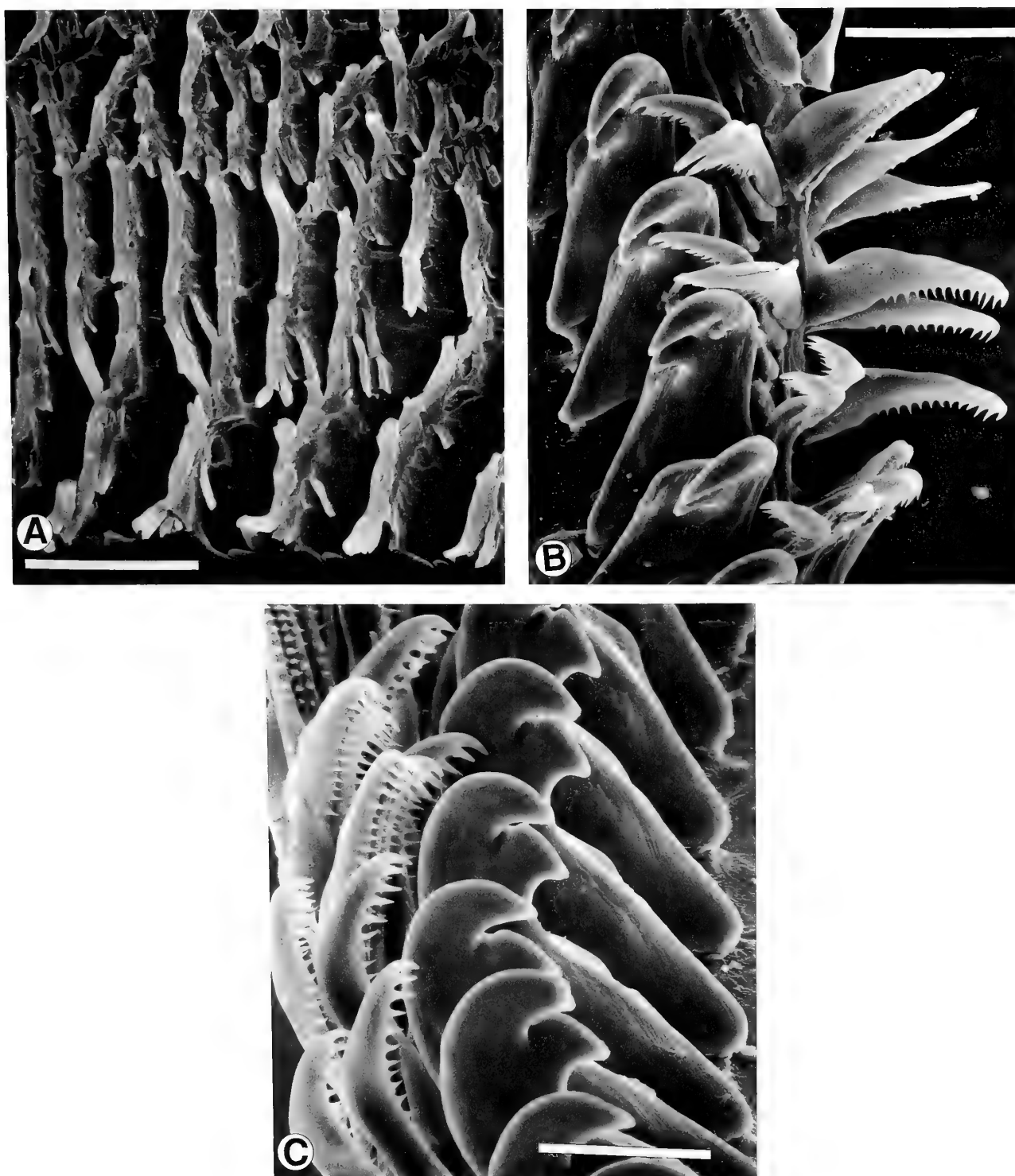


Figure 23

Hallaxa indecora (Bergh, 1905). Scanning electron micrographs, CASIZ 084863. A. Jaw rodlets, scale = 20 μm . B., C. Inner and outer lateral teeth, B. scale = 43 μm , C. scale = 30 μm .

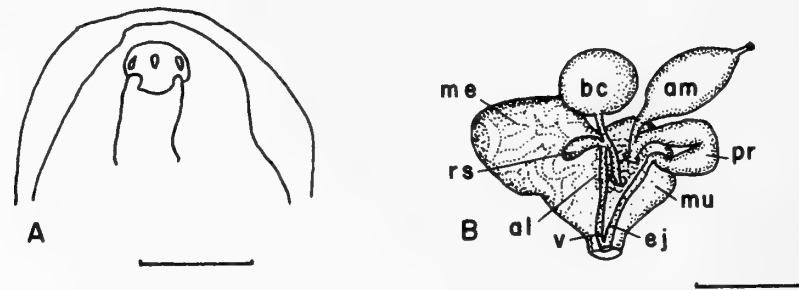


Figure 24

Hallaxa hileenae Gosliner & Johnson, sp. nov. A. Camera lucida line drawing of ventral view of head and foot of preserved specimen, scale = 1.0 mm. B. Reproductive system, al- albumen gland, am- ampulla, bc- bursa copulatrix, ej- ejaculatory portion of vas deferens, me- membrane gland, mu- mucous gland, pr- prostatic portion of vas deferens, rs- receptaculum seminis, v- vagina, scale = 0.5 mm.

assisted in our field work in Papua New Guinea, and collected the first specimen of *Hallaxa iju* from there. Hileen is the Papua New Guinea pidgin name for Eileen.

External morphology: The living animals (Figure 1F) are 5–12 mm in length. The general body color is a wine red. Opaque white pigment is present around the margins of the notum and gills, and on the elevated ridges of the notum. There is also scattered opaque white pigment around the club of the rhinophores, and more densely at their apex. The white pigment is most dense in the outer marginal areas of the notum. The submarginal areas of the notum between the ridges contain irregular charcoal gray to black markings and a few scattered opaque white spots.

The body is elongate and ovoid. A thick longitudinal ridge extends mid-dorsally from the area between the rhinophores and divides into a pair of diagonal ridges, anterior to the gills. Together these ridges form a y-shaped elevated portion of the otherwise smooth notum. The branchial plume consists of six to eight unipinnate gills. The rhinophores are bulbous with five to six lamellae. The foot (Figure 24A) is rounded anteriorly with elongate, anteriorly directed foot corners. A small pit is present on either side of the mouth.

Internal morphology: The buccal mass is short and muscular with a more anterior region of numerous oral glands. The anterior end of the muscular portion contains a ring of labial armature. The labial armature (Figure 25A) contains numerous rows of multifid rodlets, each consisting of three to five denticles. The radular formula is $21 \times 5.1.0.1.5$ and $24 \times 7-8.1.0.1.7-8$ in the two paratypes examined. The inner lateral teeth (Figure 25B, C) are broad and thick with two large, curved cusps on their inner edge. There are no secondary denticles on the inner laterals. The five to eight outer lateral teeth are narrow and elongate, all of similar size and shape (Figure 25C, D). They bear 9–12 elongate denticles. There are slightly fewer denticles on the outermost teeth.

The reproductive system (Figure 24B) is triaulic. The short pre-ampullary duct is narrow and expands into a

saccate ampulla. The ampulla narrows and divides into a short oviduct and the vas deferens. The vas deferens is prostatic proximally. It is curved and narrows distally into a thinner ejaculatory segment. The muscular ejaculatory portion terminates at the gonopore adjacent to the vagina. The vagina is thin and moderately elongate. It joins the small, pyriform receptaculum seminis. Together these ducts connect with the moderately short uterine and bursa copulatrix ducts. The bursa copulatrix is spherical and thin-walled. The uterine duct enters the female gland mass at the albumen gland. The membrane gland is distinct from the remainder of the female gland mass and consists of numerous tubules. The mucous gland is smooth throughout its surface.

Discussion: *Hallaxa hileenae* is immediately distinguishable from other members of the genus by its purple color with black maculations and the distinct y-shaped ridge present on the notum. It is most similar to *H. indecora*, but differs in several external and internal regards (see discussion of *H. indecora*). *Hallaxa hileenae* is a member of the derived subclade of species with bicuspidate inner lateral teeth lacking smaller denticles. Members of this group also have a membrane gland that is a lobe separated from the remainder of the female gland mass.

Hallaxa cryptica Gosliner & Johnson, sp. nov.

(Figures 1G, 26–29)

Type material: Holotype: (white form), CASIZ 085935, Devil's Pt., Maricaban Island, off Batangas Bay, off Luzon Island, Philippines, 3 m depth, 26 March 1993, T. M. Gosliner. Paratypes: One specimen (purple form), Bernice P. Bishop Museum, Honolulu, BPBM 9941, under dead coral head, Ananij Pinnacle ($11^{\circ}28'8''N$, $182^{\circ}22'30''E$), Enewetak Atoll, Marshall Islands, 10 m depth, 10 September 1981, S. Johnson. One specimen (purple form), CASIZ 083764, dissected, Arthur's Rock, Maricaban Peninsula, s. end Luzon Island, Philippine Islands, 15 m depth, 22 February 1992, T. M. Gosliner. One specimen (white form), BPBM 9942, under dead coral head, K-9 Pinnacle,

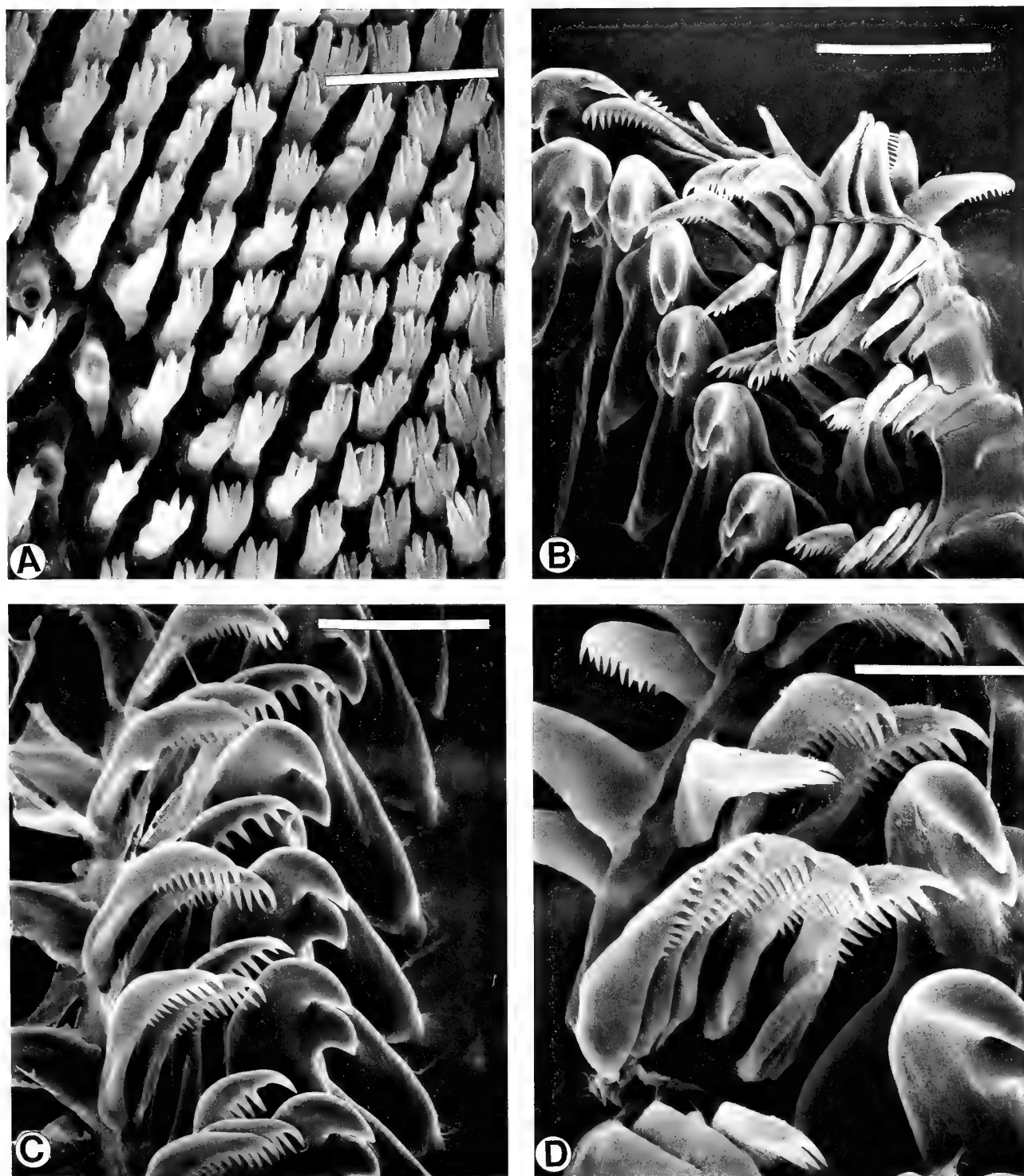


Figure 25

Hallaxa hileenae Gosliner & Johnson, sp. nov. Scanning electron micrographs, CASIZ 086402. A. Jaw rodlets, scale = 15 μ m. B. Half row of radular teeth, scale = 60 μ m. C. Inner and outer lateral teeth, scale = 43 μ m. D. Outer lateral teeth, scale = 25 μ m.

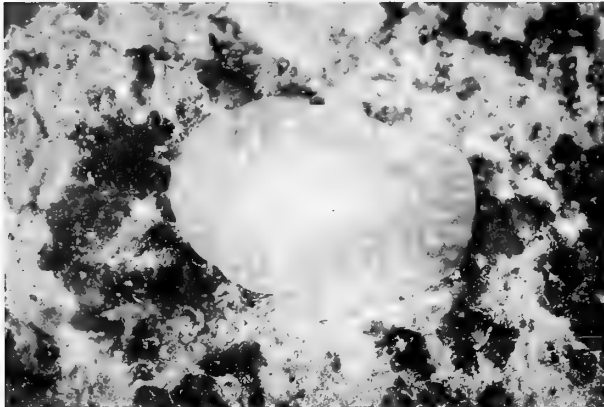


Figure 26

Hallaxa cryptica Gosliner & Johnson, sp. nov. Living animal of white color form, Philippines.

Kwajalein Atoll, Marshall Islands, 8 m depth, 19 September 1982, S. Johnson. One specimen (white form), CASIZ 088351, Enewetak Atoll, Marshall Islands, 16 September 1982, S. Johnson. Two specimens (white form), one dissected, CASIZ 088352, Enewetak Atoll, Marshall Islands, 30 July 1983, S. Johnson. One specimen (white form), dissected, CASIZ 088353, Enewetak Atoll, Marshall Islands, 5 November 1988, S. Johnson.

Distribution: This species has been collected from the Marshall Islands and the Philippine Islands.

Etymology: The name *cryptica* refers to the cryptic coloration of this species on its sponge prey.

External morphology: The living animals are 7–25 mm in length with a rounded body shape. The general body color is variable and may be either creamy yellowish white (Figure 26A) or, less commonly, light purple brown (Figure 1G). The purple form may have darker purple flecks. Both forms have scattered opaque white spots that appear

as tubercles, but are not elevated from the notum. Whitish specimens may also have light tan streaks and spots perpendicular to the notal margin. The rhinophores and gills are the same color as, or slightly darker than, the general body color. Purple specimens have a white tip at the apex of the rhinophores. The branchial plumes consist of 8–15 unipinnate gills. The rhinophores are bulbous with five to nine lamellae. The foot (Figure 27A) is concavely curved anteriorly with broad, anteriorly directed foot corners. A small pit is present at the lateral margins of the mouth and head.

Internal morphology: The buccal mass consists of a short muscular region and a more elongate, anterior glandular region. The labial cuticle consists of a ring of jaw elements at the anterior end of the muscular portion of the buccal mass. The jaw elements (Figure 28A) consist of numerous rows of rodlets, each with one to three denticles along its margin. The radular formula in two purple specimens is $21 \times 9-10.1.0.1.9-10$ and $25 \times 7.1.0.1.7$, and $34 \times 14.1.0.1.14$ (Figure 28B) in the one white specimen examined. The inner lateral teeth (Figures 28C, D, 29A) are broad and thick in specimens of both color forms. The inner edge of the free portion of the inner laterals is curved and bifid, without secondary denticles. The outer lateral teeth are narrow basally, and elongate. The outermost teeth are shorter than the more inner ones. The outer laterals bear 6–12 denticles along their inner margin (Figure 29B).

The reproductive system (Figure 27B) is triaulic. The pre-ampullary duct widens to a broad, saccate ampulla. The ampulla narrows and bifurcates into the short oviduct and the vas deferens. The vas deferens widens into the proximal prostatic portion. This prostatic segment curves and narrows into the straight, muscular ejaculatory portion. The ejaculatory segment exits at the gonopore, adjacent to the vagina. The vagina is thin and elongate. It joins the base of the duct of the pyriform receptaculum seminis. These ducts join with the short uterine duct and

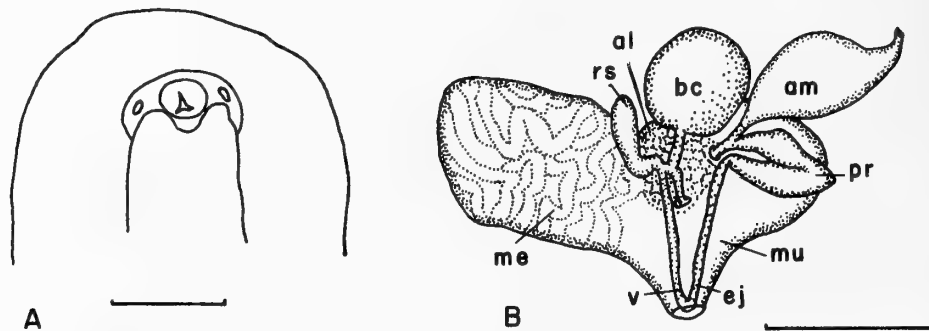


Figure 27

Hallaxa cryptica Gosliner & Johnson, sp. nov. A. Camera lucida line drawing of ventral view of head and foot of preserved specimen, scale = 1.0 mm. B. Reproductive system, al- albumen gland, am- ampulla, bc- bursa copulatrix, ej- ejaculatory portion of vas deferens, me- membrane gland, mu- mucous gland, pr- prostatic portion of vas deferens, rs- receptaculum seminis, v- vagina, scale = 0.75 mm.

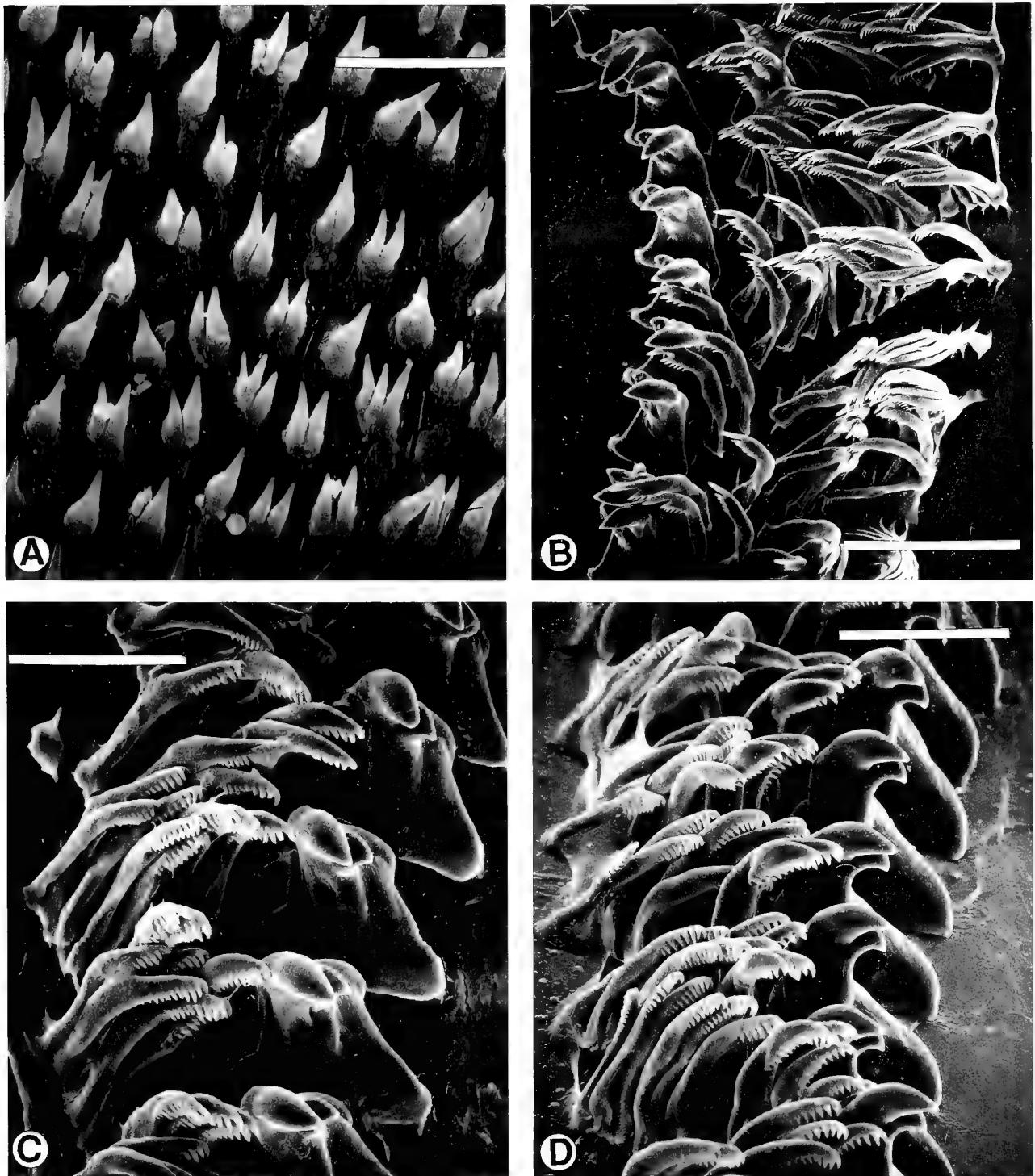


Figure 28

Hallaxa cryptica Gosliner & Johnson, sp. nov. Scanning electron micrographs. A. Jaw rodlets, purple specimen, Philippines, CASIZ 083764, scale = 15 μm . B. Half row of teeth, white specimen, Enewetak, CASIZ 088352, scale = 100 μm . C. Half row of teeth, purple specimen, Enewetak, BPBM 9941, scale = 60 μm . D. Half row of teeth, purple specimen, Philippines, CASIZ 083764, scale = 60 μm .

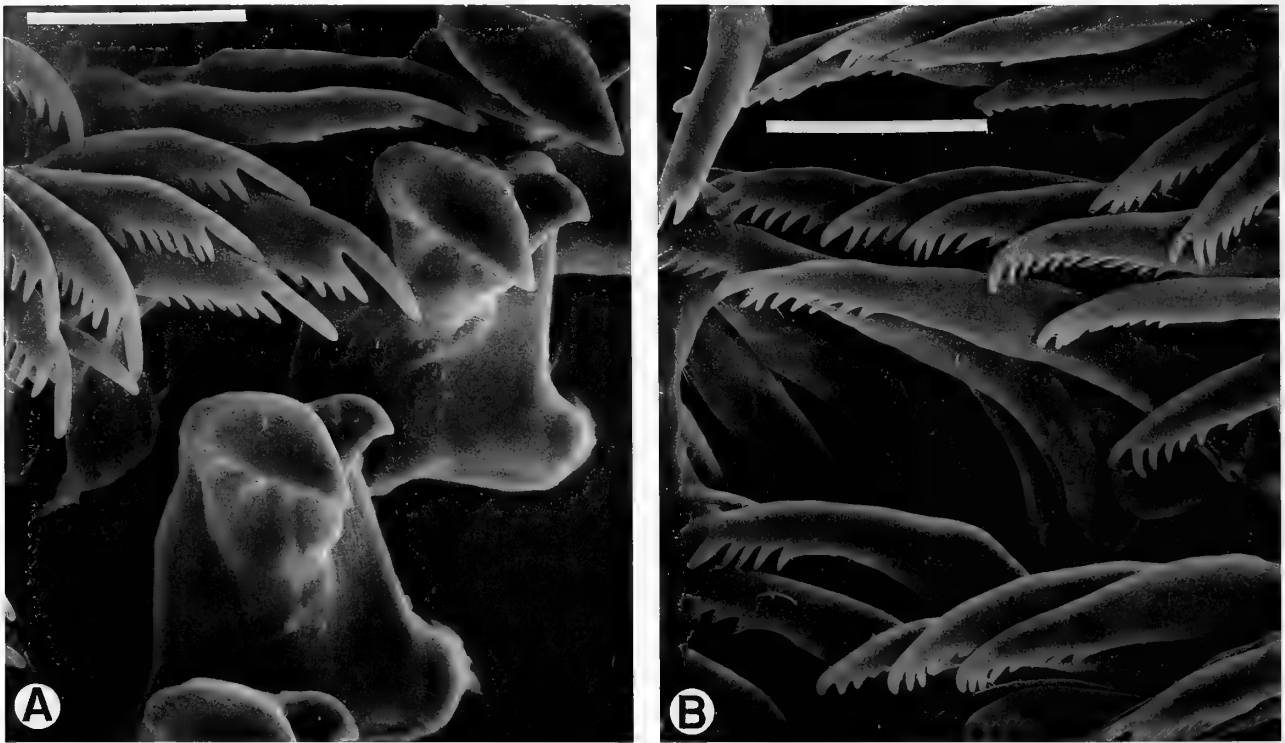


Figure 29

Hallaxa cryptica Gosliner & Johnson, sp. nov. Scanning electron micrographs. A. Inner lateral teeth, white specimen, Enewetak, CASIZ 088352, scale = 30 μ m. B. Outer lateral teeth, white specimen, Enewetak, CASIZ 088352, scale = 30 μ m.

the slightly longer duct of the bursa copulatrix. The bursa is large, thin-walled, and spherical. The uterine duct enters the female gland mass within the albumen gland. The mucous gland is large with numerous tubercles. It is a distinct lobe, separated laterally from the albumen and membrane glands.

Discussion: There are no apparent differences, either external or internal, between purple and white specimens, other than those relating to color. *Hallaxa cryptica* is most similar to *H. translucens* and *H. paulinae* in general appearance. All three species are cryptic in appearance and have a broad body shape, but differ in important aspects of their anatomy. These differences are discussed in detail in the discussions of the two other taxa. The anatomy of the reproductive system suggests closer affinities of *H. cryptica* to *H. indecora*, *H. hileenae* and *H. michaeli* than to *H. translucens* or *H. paulinae*. *H. cryptica*, *H. indecora*, *H. hileenae* and *H. michaeli* have a lobed membrane gland that is well-separated from the remainder of the female gland mass.

Hallaxa michaeli Gosliner & Johnson, sp. nov.

(Figures 1H, 30, 31)

Hallaxa indecora Burn, 1958:27, not Bergh, 1905.

Material: Holotype, AM C.174884, Bateman's Bay, New South Wales, Australia, intertidal, 19 December 1984, M. L. Gosliner.

Distribution: This species is known from the type locality in New South Wales and Victoria (Burn, 1958), Australia.

Etymology: This species is named for Michael Gosliner, who collected the holotype specimen of this species.

External morphology: The living specimen (Figure 1H) is 6 mm in length, elongate and ovoid in shape. It is uniformly dirty translucent yellowish white with a few scattered opaque white specks. The notum is smooth and devoid of tubercles. The apex of the rhinophores is also opaque white. There are nine unipinnate gills and seven lamellae on either rhinophore. The foot (Figure 30A) is rounded anteriorly with broad, triangular, anteriorly directed foot corners. A pit is present near the lateral margin of either side of the head.

Internal morphology: The buccal mass is elongate with the anterior portion being highly glandular. The labial cuticle consists of numerous multifid rodlets (Figure 31A). The radular formula in the single specimen is $27 \times 6-8.1.0.1.6-8$ (Figure 31B, C). The inner lateral teeth (Figure 31D) are broad and thick. Their free edge contains a pair of curved cusps. No auxiliary denticles are present.

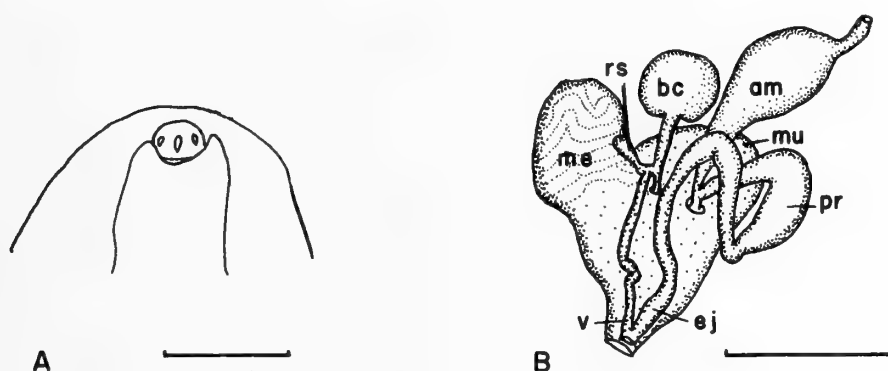


Figure 30

Hallaxa michaeli Gosliner & Johnson, sp. nov. A. Camera lucida line drawing of ventral view of head and foot of preserved specimen, scale = 1.0 mm. B. Reproductive system, am- ampulla, bc- bursa copulatrix, ej- ejaculatory portion of vas deferens, me- membrane gland, mu- mucous gland, pr- prostatic portion of vas deferens, rs- receptaculum seminis, v- vagina, scale = 1.0 mm.

The outer lateral teeth (Figure 31B, C) are narrow and elongate with the outermost teeth being slightly shorter than the inner ones. The innermost outer laterals have 9–10 triangular denticles on their inner face. The outermost ones have six to eight denticles.

The reproductive system (Figure 30B) is triaulic. The narrow pre-ampullary duct widens to a short, thick ampulla. The ampulla narrows and bifurcates into the short oviduct and the vas deferens. The proximal part of the vas deferens is prostatic. It curves and narrows into the ejaculatory portion. The ejaculatory segment is elongate and forms one elongate loop. It terminates at the gonopore, adjacent to the vagina. The vagina is elongate and slightly convoluted. It joins the small, digitiform receptaculum seminis. Together these ducts join the short uterine duct and more elongate duct of the bursa copulatrix, after a short distance. The membrane gland consists of many tubules and is a lobe distinct from the albumen and mucous glands.

Discussion: Burn (1958) described the external morphology of the specimen from Victoria, Australia, which he called *Hallaxa indecora* Bergh. The pale yellow body color is similar to the type specimen of *H. michaeli*. The remaining features of gill and rhinophoral lamellae number are similar to those described here. Burn also described the presence of structures on the sides of the mouth that he thought might be degenerate oral tentacles. These agree with the vestigial tentacular pits described here for *H. michaeli* (Figure 27A). It is highly likely that Burn's specimen is *H. michaeli*, but this must be verified by examination of its internal anatomy.

Despite the fact that only a single specimen of this species was examined, it is sufficiently distinct to warrant description. It differs in its coloration from the other species that have only two large cusps without secondary denticles on the inner lateral teeth. *Hallaxa cryptica* may also be whitish in color, but it has large opaque white spots, a

broader body, and more elongate outer lateral teeth. *Hallaxa michaeli* is unique in having a more elongate vas deferens than other members of the genus.

DISCUSSION

A. Significance to doridaean phylogeny

Cryptobranchs are dorid nudibranchs that have the derived feature of possessing a circle of gills that can be withdrawn into a branchial cavity below the surface of the mantle. Other groups of dorids have a circle of gills, but they cannot be withdrawn into a protective pocket. Phanerobranchs and gnathodorids (*Bathydoris* and *Doriodoxa*) have plesiomorphically thickened, chitinous jaws with or without jaw rodlets, while the cryptobranchs have more derived jaws reduced to a small area that may contain some chitinous rodlets. Wägele (1989) has suggested that bathydorids may be the sister taxon of the remainder of the Doridacea. Certainly, detailed analysis of nudibranch phylogeny, using a wide array of features, is needed to shed more light on dorid phylogeny. This requires more detailed examination of doridaeans as well as less derived members of the outgroups of dorids, dendronotaceans, arminaceans, aeolidaceans, and notaspideans.

The systematics of the cryptobranch dorid nudibranchs has been the source of controversy and disagreement since Bergh (1892) presented his classification of the Nudibranchia. Other classifications have been suggested, including the works of Thiele (1931) and Franc (1968). Kay & Young (1969) considered a series of dorid subfamilies, based on anatomical and ecological information. However, their treatment was restricted to dorid taxa present in the Hawaiian Islands. There have been few major monographic revisions of large groups of cryptobranch dorids in the last half century. An exception is the review of the kentrodorid genera *Kentrodoris* and *Jorunna* (Ev. Marcus, 1976).

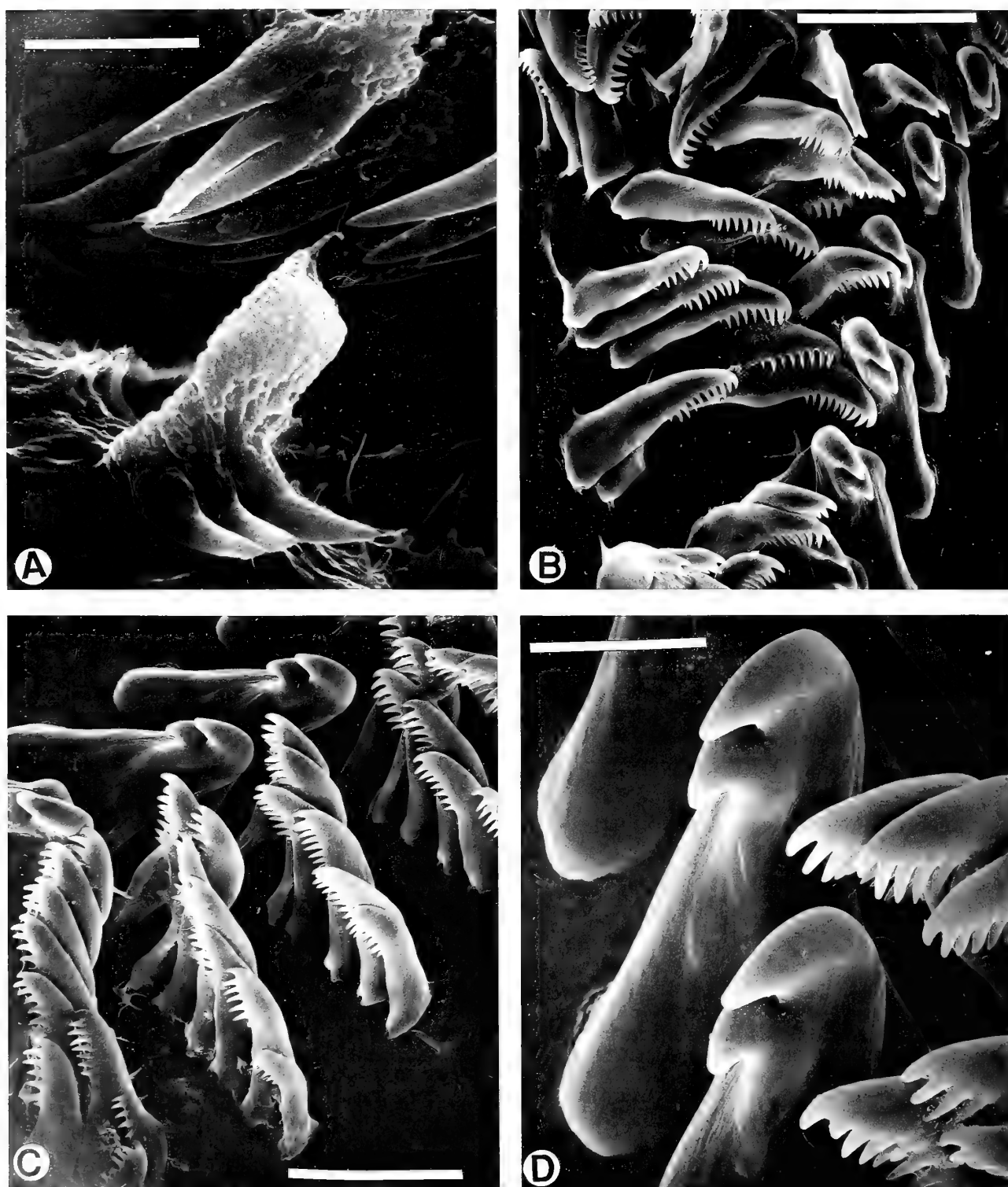


Figure 31

Hallaxa michaeli Gosliner & Johnson, sp. nov. Scanning electron micrographs, holotype, CASIZ 071472. A. Jaw rodlets, scale = 5 μm . B. Half row of radular teeth, scale = 38 μm . C. Half row of radular teeth, scale = 30 μm . D. Inner lateral tooth, scale = 13.6 μm .

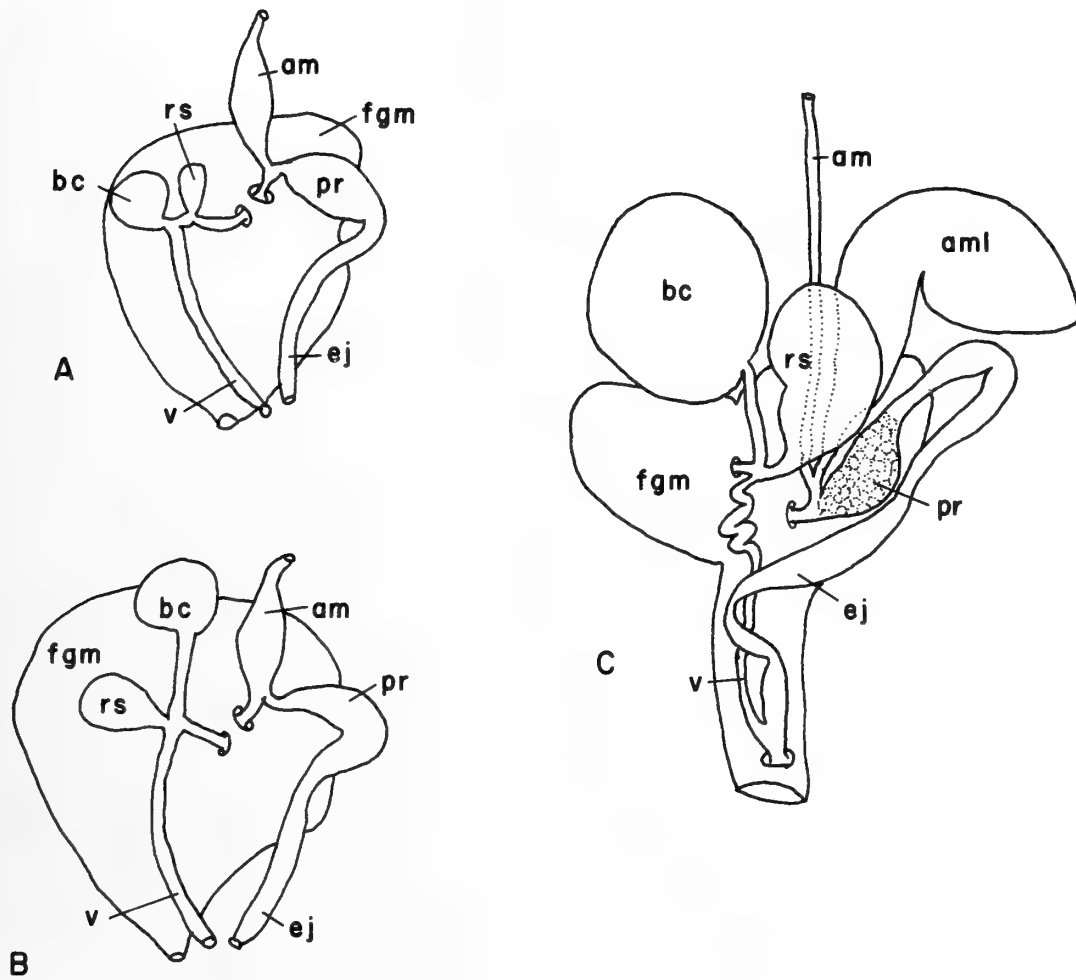


Figure 32

Dorid reproductive systems. A. Cryptobranch with serial arrangement. B. *Hallaxa* with semi-serial arrangement. C. *Actinocyclus japonicus* (Eliot, 1913), with semi-serial arrangement. am- ampulla, bc- bursa copulatrix, ej- ejaculatory portion of vas deferens, fg- female gland mass, pr- prostatic portion of vas deferens, rs- receptaculum seminis, v- vagina, not to scale.

The first comprehensive treatment of cryptobranch dorids in recent times is the generic revision of the Chromodorididae undertaken by Rudman (1984). He evaluated polarities of evolutionary change in chromodorids and revised the generic distinctions, but did not evaluate the limits of genera based on strictly cladistic methodology. He studied polarity of character evolution in chromodorids, but did not evaluate whether the genera he circumscribed were monophyletic or diagnosed on the bases of synapomorphic features. Nevertheless, Rudman's treatment of chromodorid classification represents the first comprehensive treatment of dorid classification employing a wide variety of characters from different organ systems.

In his discussion of dorid evolution, Rudman noted that chromodorids are unique in their arrangement of reproductive organs. Virtually all other dorids have a serial arrangement of reproductive organs. In this configuration,

the uterine duct connects to the receptaculum seminis and joins the receptaculum to the base of the bursa copulatrix (Figure 32A). The vagina emerges from the base of bursa and exits at the gonopore, adjacent to the penis. This is the plesiomorphic arrangement within the dorids and is also present in most notaspideans (Willan, 1987), the likely sister taxon of the Doridacea. In chromodorids, the duct from the receptaculum enters the mid-region of the vagina. An arrangement of reproductive organs similar to that of chromodorids is found in several species of *Hallaxa* (Figure 32B) and *Actinocyclus japonicus* (Eliot, 1913) (Figure 32C). In these taxa, the uterine duct joins the middle of the vaginal duct. This is a derived feature shared only by members of the Chromodorididae and Actinocyclusidae. Contrary to most other dorids, members of these taxa also are known to feed largely upon sponges that lack spicules (Rudman, 1984; Goddard, 1984). The radulae of chro-

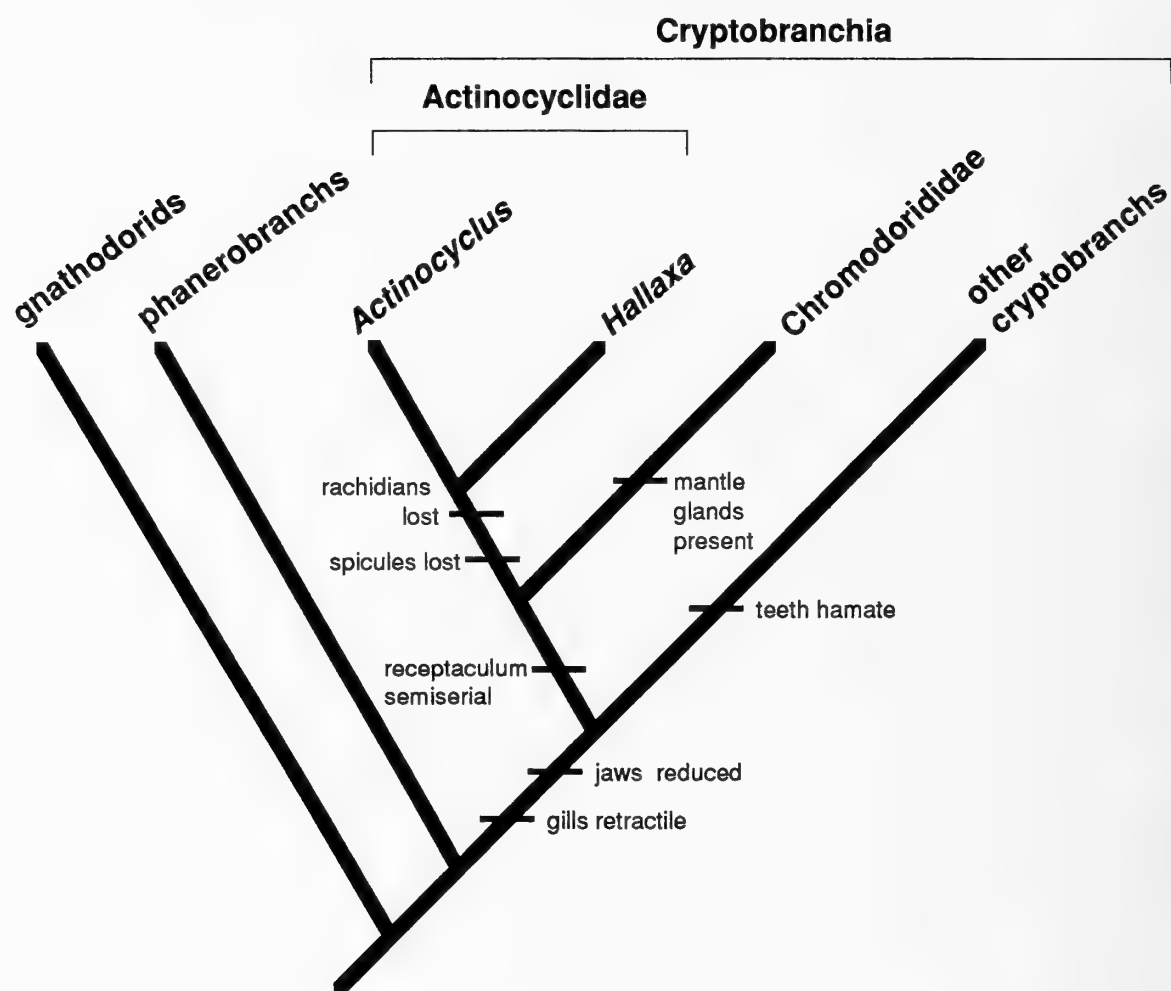


Figure 33

Hypothesized phylogeny of Doridacea.

modorids and actinocyclids are similar in having a large primary cusp with numerous smaller denticles along the margins of the teeth. This form of radular teeth also appears to be derived rather than ancestral, based upon outgroup comparisons with phanerobranch and gnathodorid dorids and notaspideans. The remainder of the cryptobranchs have simply hamate teeth, which appears to represent another derived form when compared to outgroups. Based on their similar derived reproductive and radular morphology, it appears that chromodorids and actinocyclids are more closely related to each other than to any other cryptobranch dorids. Rudman also demonstrated that many chromodorids retain a rachidian row of teeth; this is a plesiomorphic arrangement within the chromodorids. Species of *Bathydoris* (Wägele, 1989) and some phanerobranchs also have a rachidian row of teeth, and this appears to represent the plesiomorphic arrangement within the Doridacea. The fact that the vestiges of rachidian teeth are found only in some chromodorids, but not in any other

cryptobranchs, suggests that the chromodorid-actinocyclid clade is divergent from the remainder of the Cryptobranchia. Most other systematic treatments have considered chromodorids and actinocyclids as highly derived cryptobranchs. Chromodorids have well-developed dermal defensive glands that are unique to members of this taxon. Actinocyclids share two derived features absent in the least derived members of their sister group, the Chromodorididae; the rachidian teeth are absent and the notum lacks spicules. The phylogenetic hypothesis suggested here for cryptobranch dorid nudibranchs is summarized in Figure 33.

B. Morphological variability and character polarity

Few morphological studies have been undertaken within the Actinocyclidae. The only description of reproductive morphology of a species of *Actinocyclus* is that of *A. japonicus* (Eliot, 1913) by Kay & Young (1969). Specimens of *A. japonicus* and three previously described species of

Hallaxa, *H. apesae*, *H. chani*, and *H. indecora* were examined to confirm described morphological variability. Morphology of *H. gilva* and *H. decorata* were based only upon their original descriptions.

In order to ascertain the polarity of morphological change within *Hallaxa*, *Actinocyclus* and chromodorids were considered as outgroups.

The following characters were considered:

1. Gills: Within the Actinocyclidae, all taxa possess unipinnate gills. There are 8–18 gills in *Actinocyclus japonicus* and 6–14 in species of *Hallaxa*. Several species have more gills than others, independent of their relative body size. A larger number of gills is considered plesiomorphic, based on comparisons with *Actinocyclus*. It appears that the plesiomorphic arrangement of the gills in the Chromodorididae is bi-tripinnate gills.

0 = 12–15 gills; 1 = 6–11 gills.

2. Body shape: In *Hallaxa*, some specimens have a round, ovoid body shape, while others are far narrower and more elongate. Species of *Actinocyclus* and less derived chromodorids are round in shape. This shape is considered plesiomorphic for *Hallaxa*.

0 = round body shape; 1 = ovoid to elliptical body shape.

3. Tubercles: Species of *Actinocyclus* and some *Hallaxa* have large rounded tubercles scattered over the surface of the notum. These tubercles do not appear to be supported by spicules. Other species of *Hallaxa* have either small tubercles or an entirely smooth notum. Possessing large tubercles is considered plesiomorphic in *Hallaxa*, with small tubercles being derived from large, and a smooth notum derived from one with small tubercles. A few chromodorids of the least derived genera *Cadlina* and *Tyrinna* have many large tubercles. This appears to be an ordered character with the following transformation series 0–1–2.

0 = many, large tubercles; 1 = few small tubercles; 2 = smooth notum.

4. Rhinophoral lamellae: In *Actinocyclus*, chromodorids, and most species of *Hallaxa*, the rhinophoral lamellae are simple ridges, extending a short distance out from the clavus. In *H. iju*, the lamellae extend outwards for at least twice the distance of those of other species. This elaboration is considered autapomorphic.

0 = short lamellae; 1 = extended lamellae.

5. Rhinophoral shape: The majority of dorid nudibranchs, including the Chromodorididae, *Actinocyclus* and *Hallaxa*, have bulbous rhinophores. *Hallaxa paulinae* is unique in having conical rhinophores with few lamellae. This is considered as an autapomorphy for *H. paulinae*.

0 = bulbous rhinophores; 1 = conical rhinophores.

6. Oral tentacles: In *Actinocyclus* and chromodorids, a short oral tentacle is present on either side of the mouth. Its form is variable in chromodorids (Rudman, 1984), but either grooved or digitiform tentacles are present in all taxa. In some species of *Hallaxa*, reduced oral tentacles

may be present, or a small pit may be found on either side of the head. These pits are considered to represent vestiges of the oral tentacles and represent a derived condition within the Actinocyclidae.

0 = oral tentacles present; 1 = oral pits present.

7. Foot: In chromodorids and most other cryptobranch dorids, the anterior margin of the foot is slightly rounded with the anterolateral margins extending laterally. This form is also present in some species of *Hallaxa*. In the remaining species of *Hallaxa*, the lateral margins of the foot are directed anteriorly. Species of *Actinocyclus* have an arrangement of the foot similar to that found in the species of *Hallaxa* with anteriorly directed foot margins. However, in *Actinocyclus*, the margins almost entirely surround the mouth and oral tentacles. Also, there appears to be a secondary thickening near the anterior margin of the foot. A straight foot appears to be the ancestral condition in *Hallaxa* and most other dorids. Subsequent character analysis indicates that the derived forms present in some species of *Hallaxa* and *Actinocyclus* represent independently derived modifications of the ancestral configuration and are here treated as unordered.

0 = straight foot margin; 1 = concave foot margin; 2 = rounded foot margin with thickening.

8. Jaw armature: All chromodorids and all species of *Actinocyclus* and *Hallaxa* have a pair of narrow bands of rodlets along the anterior margin of the labial cuticle. In *Hallaxa* sp., there are only three to four rows of rodlets forming a thin band of armature along the jaws. All other species have multiple rows (at least 10), which is considered plesiomorphic for the chromodorid-actinocyclid clade. A reduced number of rows of rodlets is autapomorphic for *Hallaxa* sp.

0 = more than 10 rows of rodlets; 1 = 3–4 rows of rodlets.

9. Jaw rodlets: In species of *Actinocyclus* and some species of *Hallaxa*, the jaw rodlets are simple, undivided hooks. Most chromodorids have divided rodlets. In most species of *Hallaxa*, the rodlets have multifid apices. This latter form is considered the derived form within the Actinocyclidae.

0 = undivided rodlets; 1 = divided rodlets.

10. Outer lateral teeth: The radula of most chromodorids and *Actinocyclus* is broad, with numerous lateral teeth per row. In *Actinocyclus*, there are 20–30 outer lateral teeth on either side of the radula. In contrast, species of *Hallaxa* have 4–22 outer lateral teeth per half row. Species with fewer outer lateral teeth are considered to be more derived than species with many teeth.

0 = 13–22 outer laterals/side; 1 = 4–11 outer laterals/side.

11. Outer lateral shape: In chromodorids, *Actinocyclus*, and most species of *Hallaxa*, the outer lateral teeth are all comb-shaped. *Hallaxa elongata* is unique in having outer

lateral teeth that are similar to the inner lateral teeth in shape. This is considered to represent an autapomorphy in *H. elongata*.

0 = comb-shaped outer laterals; 1 = cuspidate outer laterals.

12. Inner lateral cusp: The inner lateral teeth of species of *Actinocyclus* and some species of *Hallaxa* have a single rounded-to-pointed cusp with small denticles along the outer side of the tooth. In other species of *Hallaxa*, the bifid primary cusp is bifid and planar on the inner edge of the tooth. This planar, bifid cusp is considered apomorphic within the Actinocyclusidae. A bifid cusp is present in the highly derived chromodorid genus *Hypselodoris* and other species of *Hallaxa*. The bifid cusp in these taxa is not planar and appears to have originated independently.

0 = multiplanar cusps; 1 = bifid, planar cusp.

13. Inner lateral shape: Species of *Actinocyclus* and most species of *Hallaxa* have inner lateral teeth that are markedly broader than the adjacent outer lateral teeth. This is also true of many chromodorids in the genera *Cadlina* and *Noumea*. In *H. sp.* the inner lateral teeth are thin and not markedly different from the outer laterals. This appears to be an autapomorphy for *H. sp.*

0 = inner lateral broad; 1 = inner lateral narrow.

14. Inner lateral dentition: The inner lateral teeth of most chromodorids, *Actinocyclus*, and most species of *Hallaxa* have smaller denticles on the outside of the primary cusp. In several species of *Hallaxa* with a bifid, planar cusp on the inner lateral teeth, secondary denticles are entirely absent. This is considered a derived feature.

0 = secondary denticles present; 1 = secondary denticles absent.

15. Receptaculum seminis: In many chromodorids, *Actinocyclus*, and some species of *Hallaxa*, the receptaculum seminis is situated immediately opposite the point where the uterine duct enters the vagina. The receptaculum seminis is situated more distally in other species of *Hallaxa*. This latter form is considered apomorphic.

0 = receptaculum opposite uterine duct; 1 = receptaculum situated off vagina, distal to uterine duct.

16. Vagina: In chromodorids, *Actinocyclus*, and most species of *Hallaxa*, the vaginal duct is elongate and the uterine duct joins it near the middle of its length. The uterine duct of *H. paulinae* enters the vagina far more distally. The receptaculum seminis enters the vagina even more distally, close to the common gonopore. This arrangement is considered to be autapomorphic for *H. paulinae*.

0 = uterine duct enters middle of vagina; 1 = uterine duct enters distal portion of vagina.

17. Prostate: The vas deferens of *Actinocyclus japonicus* was described as showing no hint of a prostatic portion (Kay & Young, 1969). Two specimens examined here have a distinct prostate, restricted to the proximal end of the vas deferens (Figure 29D). All chromodorids and species

of *Hallaxa* examined have an elongate prostate that occupies the proximal third to half of the vas deferens. A prostate restricted to the proximal end of the vas deferens is found in many species of notaspideans (Ev. Marcus & Gosliner, 1984; Willan, 1987). It appears that the more restricted prostate of *Actinocyclus* is plesiomorphic for the family and that the more distal prostate of *Hallaxa* and chromodorids represent apomorphic conditions.

0 = prostate restricted to base of vas deferens; 1 = prostate found throughout proximal portion of vas deferens.

18. Vas deferens: The ejaculatory portion of the vas deferens is relatively short and straight in *Actinocyclus* and most species of *Hallaxa*. In *H. michaeli*, the ejaculatory portion is curved and more elongate. This is considered the derived condition within the Actinocyclusidae and is autapomorphic in *H. michaeli*.

0 = ejaculatory vas deferens short; 1 = ejaculatory vas deferens long.

19. Membrane gland: In chromodorids, *Actinocyclus*, and several species of *Hallaxa*, the membrane gland is adjacent to the albumen and mucous glands. In some species of *Hallaxa*, the membrane gland is separated from the albumen and membrane glands as a discrete lobe. This is considered to represent the derived condition within the Actinocyclusidae.

0 = membrane gland continuous with rest of female gland mass; 1 = membrane gland a separate lobe.

20. Ampulla: In virtually all dorids that have been studied, the ampulla is a serial tube with expanded width for storage of endogenous sperm. This is certainly true of the presumed sister groups of the Actinocyclusidae, the Chromodorididae, and all species of *Hallaxa* examined. In two specimens of *Actinocyclus japonicus* examined here, a narrow hermaphroditic duct bifurcates into the oviduct and vas deferens. Also inserting into this junction is a thick sac that stores endogenous sperm. This sac functions as the ampulla, but is separate from the hermaphroditic duct. This represents a derived feature within the Actinocyclusidae.

0 = only primary ampulla present; 1 = primary and secondary ampullae present.

C. Cladistic relationships within Actinocyclusidae

In order to develop hypotheses regarding the phylogeny of the Actinocyclusidae, the above described characters were placed in a data matrix (Table 1) and analyzed using Phylogenetic Analysis Using Parsimony, versions 2.4.1 and 3.1.1, by David Swofford. Twenty-two most parsimonious trees were produced. A consensus tree is depicted for these taxa (Figure 34). In this arrangement, a tree with a length of 38 steps and a consistency index of 0.579 was produced. In this phylogenetic hypothesis, five of the 20 characters exhibit at least one instance of reversal. These include number of gills, general body shape, dentition of the jaw rodlets, number of outer lateral teeth, and position

Table 1
Morphology of Actinocyclusidae.

	Gills	Body shape	Tubercles	Rhinophoral lamellae	Rhinophoral shape	Oral tentacles	Foot	Jaw armature	Jaw rodlets	Outer lateral teeth	Outer lateral shape	Inner lateral cusp	Inner lateral shape	Inner lateral dentition	Receptaculum seminis	Vagina	Prostate	Vas deferens	Membrane gland	Ampulla
Ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>A. japonicus</i>	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>H. aephae</i>	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0
<i>H. chani</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0
<i>H. atrotuberculata</i>	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0
<i>H. iju</i>	1	1	1	1	0	0	1	0	1	1	0	0	0	0	1	0	1	0	0	0
<i>H. elongata</i>	1	1	1	0	0	1	1	0	0	1	1	0	0	0	1	0	1	0	0	0
<i>H. albopunctata</i>	1	1	1	0	0	1	1	0	1	1	0	0	0	0	0	0	1	0	0	0
<i>H. sp.</i>	1	1	2	0	0	0	0	1	0	1	0	0	1	0	0	0	1	0	0	0
<i>H. indecora</i>	1	1	2	0	0	1	1	0	1	1	0	1	0	1	1	0	1	0	1	0
<i>H. hilleenae</i>	1	1	2	0	0	1	1	0	1	1	0	1	0	1	1	0	1	0	1	0
<i>H. cryptica</i>	0	0	2	0	0	1	1	0	1	0	0	1	0	1	1	0	1	0	1	0
<i>H. paulinae</i>	1	0	2	0	1	1	1	0	1	1	0	0	0	0	1	1	1	0	0	0
<i>H. michaeli</i>	1	1	2	0	0	1	1	0	1	1	0	1	0	1	1	0	1	1	1	0
<i>H. gilva</i>	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0
<i>H. translucens</i>	0	0	2	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0
Character number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20

of the receptaculum seminis. Three characters—body shape, loss of tubercles, and the shape of the anterior margin of the foot—exhibit one or more instances of parallelism. Seven characters are autapomorphic. The pentachotomy depicted in the consensus tree of *H. chani*, *H. translucens*, *H. gilva* and *H. atrotuberculata* is the result of ambiguities in the sequence of changes in body shape, foot shape, and jaw rodlets. One additional quadrichotomy and one trichotomy are present. Further investigation is required to resolve the ambiguities.

D. Systematic relationships

Considerable discussion has focused on the distinction between *Hallaxa* and *Actinocyclus* (Thiele, 1931; Marcus, 1957; Franc, 1968; Gosliner & Williams, 1975; Miller, 1987). Gosliner & Williams reviewed all the characters mentioned and noted that *Actinocyclus* has more rows of radular teeth, a less variable inner lateral tooth, and a broader body and foot than *Hallaxa*. Miller added that *Hallaxa* has multifid jaw rodlets and the posterior end of the foot extends beyond the posterior limit of the notum. With the study of additional species, it is apparent that these distinctions should be reexamined. Species of *Actinocyclus* clearly have almost twice the number of radular rows than any species of *Hallaxa* thus far studied. The only possible exception to this is the original description of *H. indecora*, where Bergh (1905) indicated that it had

60–65 rows of radular teeth. As indicated in the above discussion of this species, this record is dubious. The contention that the inner lateral teeth of *Actinocyclus* are less variable than those of *Hallaxa* cannot be maintained. This appears to be a species-specific character. Species of *Actinocyclus* have a consistently broader body, with more circular shape than species of *Hallaxa*. Miller's statement that *Hallaxa* species have multifid rodlets, while species of *Actinocyclus* have undivided ones, is contradicted by the presence of undivided rodlets in *H. atrotuberculata*, *H. sp.*, and *H. elongata*. It does appear that the free end of the foot of most species of *Hallaxa* extends posteriorly beyond the notum, though this is not always evident in somewhat contracted individuals. None of the above features used to distinguish the genera is apomorphic within *Actinocyclus*. All represent derivations within *Hallaxa*. This would suggest that *Actinocyclus* is paraphyletic and should not be maintained as a distinct genus. From the analysis presented here, it is apparent that *Actinocyclus* has two apomorphic features that distinguish it from *Hallaxa*, an elaboration of the anterior portion of the foot and a secondary ampulla next to the hermaphroditic duct. In addition to the above mentioned apomorphies for *Hallaxa*, the presence of an elongate prostatic portion of the vas deferens is a derived feature that distinguishes *Hallaxa* from *Actinocyclus*. It is thus concluded that both *Actinocyclus* and *Hallaxa* represent distinct monophyletic taxa.

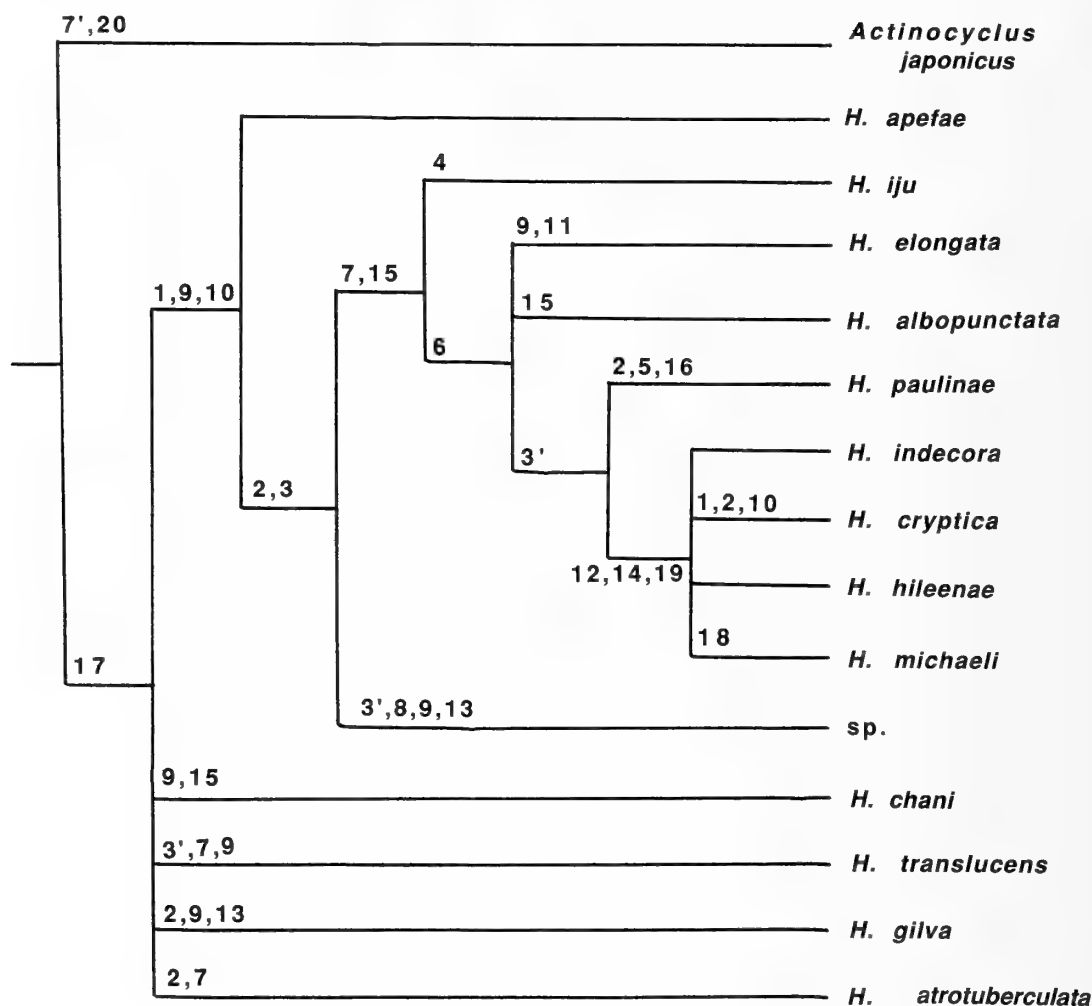


Figure 34

Hypothesized phylogeny of *Hallaxa*.

ACKNOWLEDGMENTS

This research was made possible by generous financial support from the California Academy of Sciences, the Christensen Research Institute, the Smithsonian Institution, and Katharine Stewart. We greatly appreciate the support of these institutions and individuals.

Robert Bolland and Pauline Fiene-Severns provided specimens instrumental to the completion of this work. Their time and generosity in providing specimens and photographs of Indo-Pacific opisthobranchs has greatly facilitated this and other studies. Clay Carlson, Mike Gosliner, Patty Jo Hoff, Matthew Jebb, Eveline Marcus, Gary McDonald, Brian Kensely, Mike Severns, and Eileen Sobeck also collected material crucial to the completion of this investigation. To these individuals, we extend our sincere thanks.

The final scanning electron micrographs were printed by the staff of the Photography Department of the Cali-

fornia Academy of Sciences, and the color prints of living animals were prepared by Roy Eisenhardt of the California Academy of Sciences. We are especially grateful for this assistance.

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Longshore Distribution of *Mesodesma donacium* (Bivalvia: Mesodesmatidae) on a Sandy Beach of the South of Chile

by

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Abstract. Monthly samples were taken from February 1989 to January 1990 to evaluate the longshore distribution and density of the bivalve *Mesodesma donacium* in a dissipative beach in southern Chile. The results showed that its distribution was patchy. Adult clams were confined to the surf zone, while the vast majority of juveniles occurred in the swash zone. The highest densities of adults were found in summer and autumn (up to 159 individuals per 0.25 m² in February 1989), while the minimum occurred during winter. Juveniles had similar densities all year round (up to 16-20 individuals per 0.25 m²). Most clams collected in the surf zone had similar shell lengths (70-75 mm); those collected in the swash zone were smaller than 25 mm. No relationships were found between distribution and abundances of clams and variability in textural characteristics of the surf or swash zone. Due to the limited longshore variability in grain size and sorting of sands, it is suggested that the variabilities in distribution and abundances of clams may be related to large-scale habitat characteristics rather than to small-scale textural variability.

INTRODUCTION

Macroinfaunal species living on exposed sandy beaches often show aggregated patterns of distribution. Such is the case of haustoriid amphipods (Dexter, 1971), isopods (Bally, 1983; Glynn et al., 1975), anomuran decapods such as *Emerita* (Efford, 1965; Cubit, 1969; Dillery & Knapp, 1970; Perry, 1980; Bally, 1983; Bowman & Dolan, 1985), and bivalves such as *Donax* (Loesch, 1957; Bally, 1983; McLachlan & Hesp, 1984; Sastre, 1985), *Donacilla* (McLachlan & Hesp, 1984), and *Mesodesma* (Tarifeño, 1980; Defeo et al., 1986). While some authors have suggested that biological factors (e.g., reproductive behavior) have an important role in explaining these aggregated

patterns (e.g., Efford, 1965), most have stressed the role of beach morphodynamics and/or physical characteristics in general as primary causes of patchiness in these habitats. For example, Cubit (1969) and Bowman & Dolan (1985), found that aggregations of *Emerita* are associated with beach morphology such as cusps and troughs. A similar situation was recorded by McLachlan & Hesp (1984), who found that in an Australian reflective beach, *Donacilla angusta* and *Donax parva* occurred with the highest abundances in the cusp bays.

Mesodesma donacium (Lamarck, 1818) is a typical inhabitant of the surf and subtidal zones of exposed sandy beaches of the Chilean coast (Tarifeño, 1980). This bivalve supports a fishery of high commercial value; figures from

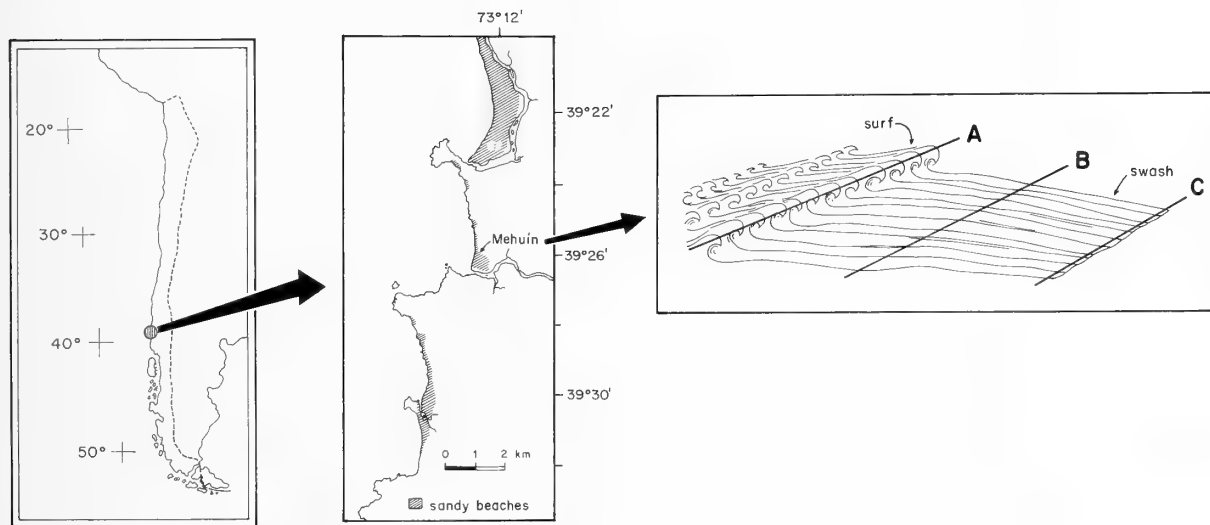


Figure 1

Location of the beach at Mehuín, southern Chile, and positions of transects A (surf zone), B, and C (upper limit of the swash run-up).

SERNAP (Servicio Nacional de Pesca) show that in the years 1988–1991, the landing of *M. donacium* in the Chilean coast has varied between 17,122 tons in 1989 and 9397 tons in 1990. In the same period, beaches located in the X Region of the country (about 40–42°S) have produced 25–58% of the annual catch (SERNAP, 1988–1991). The findings of Tarifeño (1980) for sandy beaches of Valparaíso, Chile (ca. 32°S) confirm that *M. donacium* is not evenly distributed along the coast and that its distribution might be related to longshore differences in sand-grain size. Moreover, unpublished observations have suggested that the temporal distribution of *M. donacium* in sandy beaches of the south of Chile follows a dynamic pattern.

The present study evaluates the spatial and temporal variability in the longshore distribution of *Mesodesma donacium* in southern Chile. Relationships between this variability and sand-grain size distribution are also examined.

MATERIALS AND METHODS

The sandy beach at Mehuín, Chile (39°26'S, 73°13'W) is a dissipative beach 1800 m long and fully exposed to breaking waves of the Pacific Ocean (Figure 1). Preliminary sampling of the swash zone and the near-shore edge of the breakers showed that most adult *Mesodesma donacium* (>55 mm) occurred near or just at that edge; for example, 75–90% of the adults collected during these samples (January and February 1989) came from between the breaker line and the swash zone on the beach face. Definitive collections (February 1989–January 1990) for adult clams were therefore carried out in the surf zone, which was about 1.2–1.5 m deep. One quadrat of 0.25/m² (ca. 35 cm deep) was sampled at 100-m intervals along a longshore transect covering most of the length of the beach (transect A, Figure

1). Clams were collected in a way similar to how fishermen collect *M. donacium* in the sandy beaches of south-central Chile—by twisting the feet in an area enclosed for the sampling quadrat and using the body weight to excavate the sand until clams emerged at the sediment water interface to be picked up by hand. To ensure all the clams were collected, the sediments of the sampling areas were carefully examined by hand.

Preliminary observations suggested that most juvenile *Mesodesma donacium* inhabit the mid- to high levels of the swash zone. Metallic cylinders (20 cm in diameter, 35 cm long) were used to collect sediment samples in the mid swash zone (i.e., the mid distance between the near-shore edge of the breaker zone and the upper limit of the swash run-up; transect B, Figure 1) and at the upper limit of the swash run-up (transect C, Figure 1) (one sample every other 100 m). These collections were made at the same intervals established for the surf zone (transect A). The near-shore edge of the breaker zone was also examined for juvenile clams. However, due to difficulties in using 20-cm-diameter metallic cylinders, we used PVC cylinders of 10-cm diameter (20 cm long) to collect sediment samples in the latter zone. Sediment samples collected from stations located at transects A, B, and C, and aimed to assess the distribution and abundance of juveniles, were sieved through a 1-mm-mesh sieve, the residue being carefully examined under a binocular microscope. Density data of adult and juvenile clams were expressed as the number of individuals per 0.25 m². Morisita's index of dispersion was used to measure the spatial pattern of clams. Shell-size analyses were based on anteroposterior shell lengths obtained with vernier calipers (± 0.1 mm).

A 1.7-cm-diameter plastic cylinder was used to collect sediment samples from areas close to each sampling station

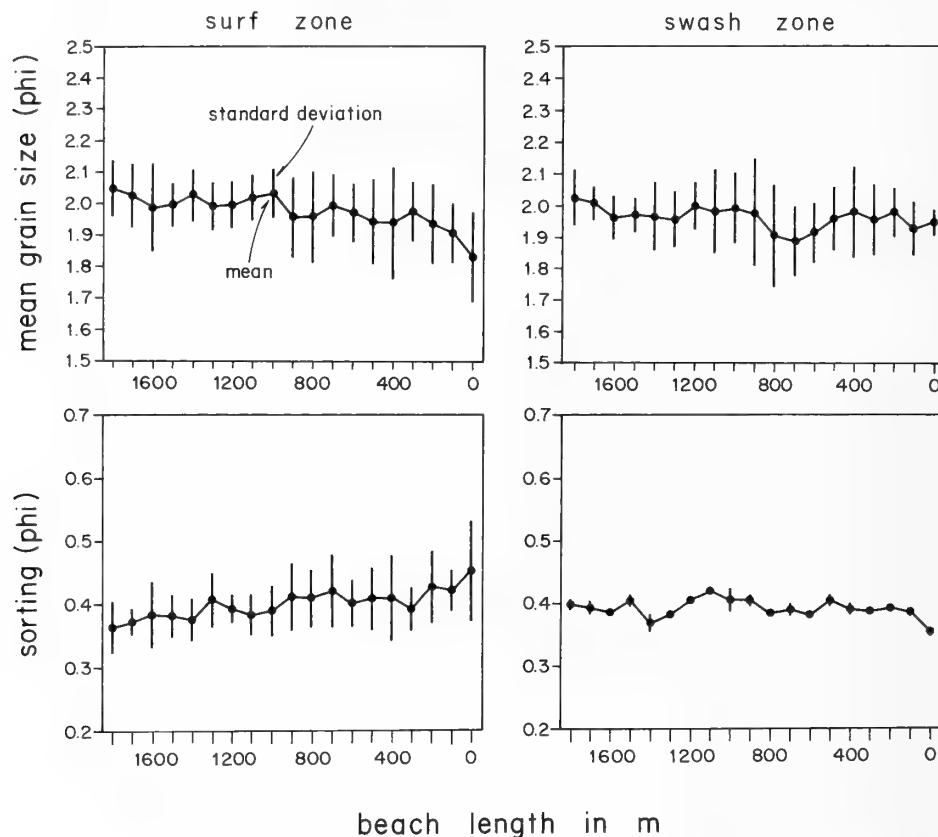


Figure 2

Spatial variability in mean sand-grain size and sorting along the surf and swash zone of the beach at Mehuín. The values are means based upon monthly measurements ($n = 12$).

to analyze relationships between clam distribution and density and textural characteristics of the sediments. Sand samples were washed with tap water to remove salts and analyzed with an Emery settling tube (Emery, 1938). Mean grain size and sorting were calculated with a moments computational method (Seward-Thompson & Hails, 1973) using a program written by Pino (1982) for a Hewlett-Packard 41 CV.

RESULTS

The sands of the surf and swash zones at the beach of Mehuín were similar in mean grain size and sorting (Figure 2). Most of the sediments can be classified as medium (1–2 phi), well-sorted sands (Folk, 1980). Mean grain size and sorting showed no longshore spatial or seasonal trend; thus, the results are presented as means for the whole period (Figure 2).

Mesodesma donacium had a discontinuous longshore distribution along the beach; that is, several clam beds were clearly distinguished during each sampling period (Figure 3). These beds were usually separated, either by areas with very low densities or by vacant areas whose lengths

ranged from 200 to 800 m. The most extensive beds were observed in February 1989, when the length of the largest bed was close to 500 m. The location of the surf areas that had the maximum densities of clams shifted throughout the study period. For example, during February 1989 the greatest densities of *M. donacium* were observed 500 m and 1500 m from the starting point (0 m) of transect A, while during May, density peaks were observed at 0 m and 600 m (Figure 3). The density of clams in the surf-zone beds were highest in February 1989, when a maximum of 159 individuals per 0.25 m² was collected at the 1500-m sampling station. High densities were also observed during May; thereafter, the population declined continuously until the following November, when the maximum density of adults was only 53 individuals per 0.25 m². Spring recovery was apparent, since low densities of clams were again observed during December and January (Figure 3).

The majority of clams collected in the surf zone (transect A) were adults. Mean shell lengths along the studied surf beds were quite similar (Figures 3, 4). The most representative size classes were 70–75 mm in shell length (Figure 3). During some months, smaller shell lengths occurred

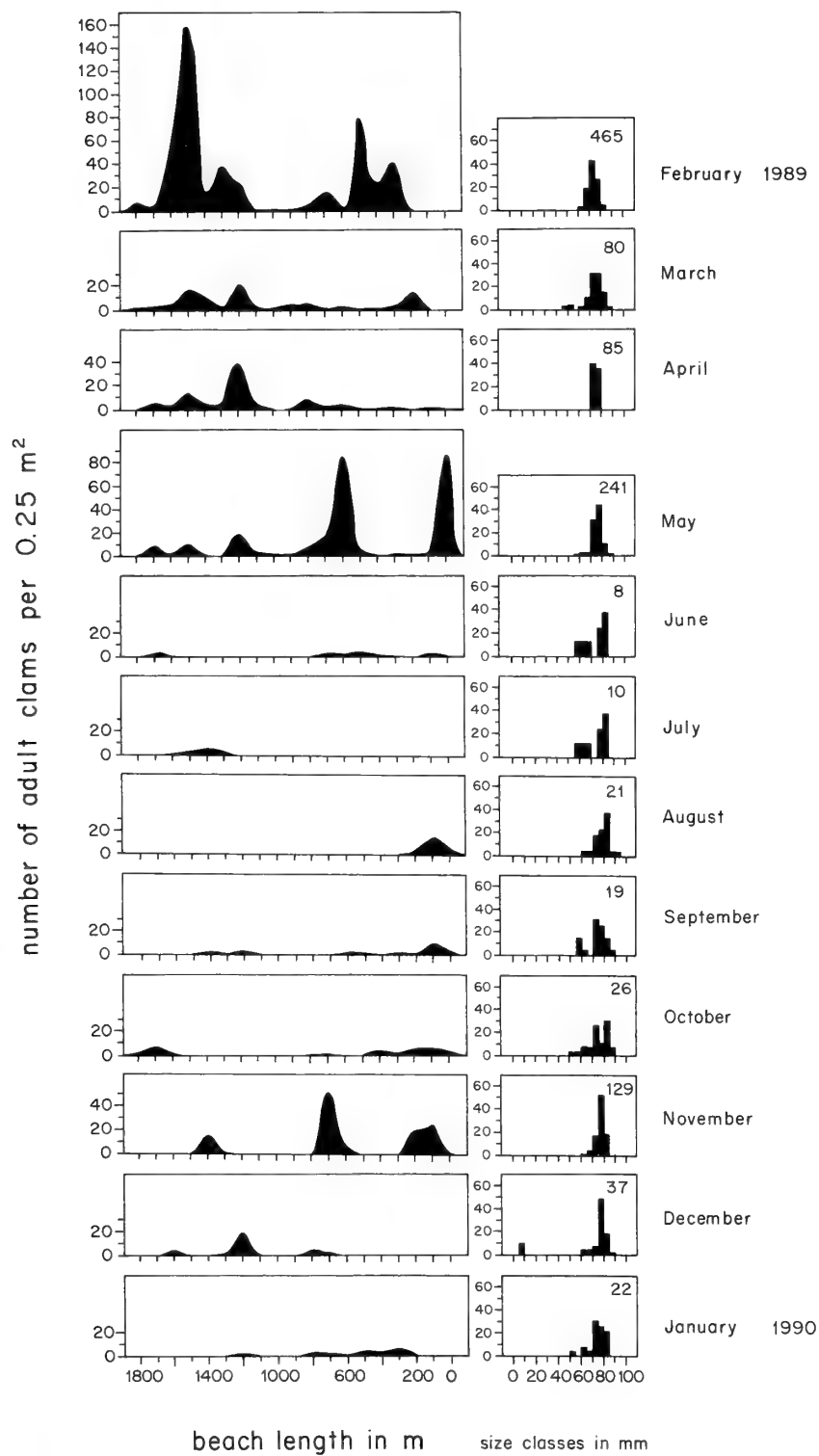


Figure 3

Spatial variability in the density of *Mesodesma donacium* along the surf zone of the beach of Mehuín. The monthly histograms show the size-class distribution (frequency in percentage) of the total number of clams collected each month.

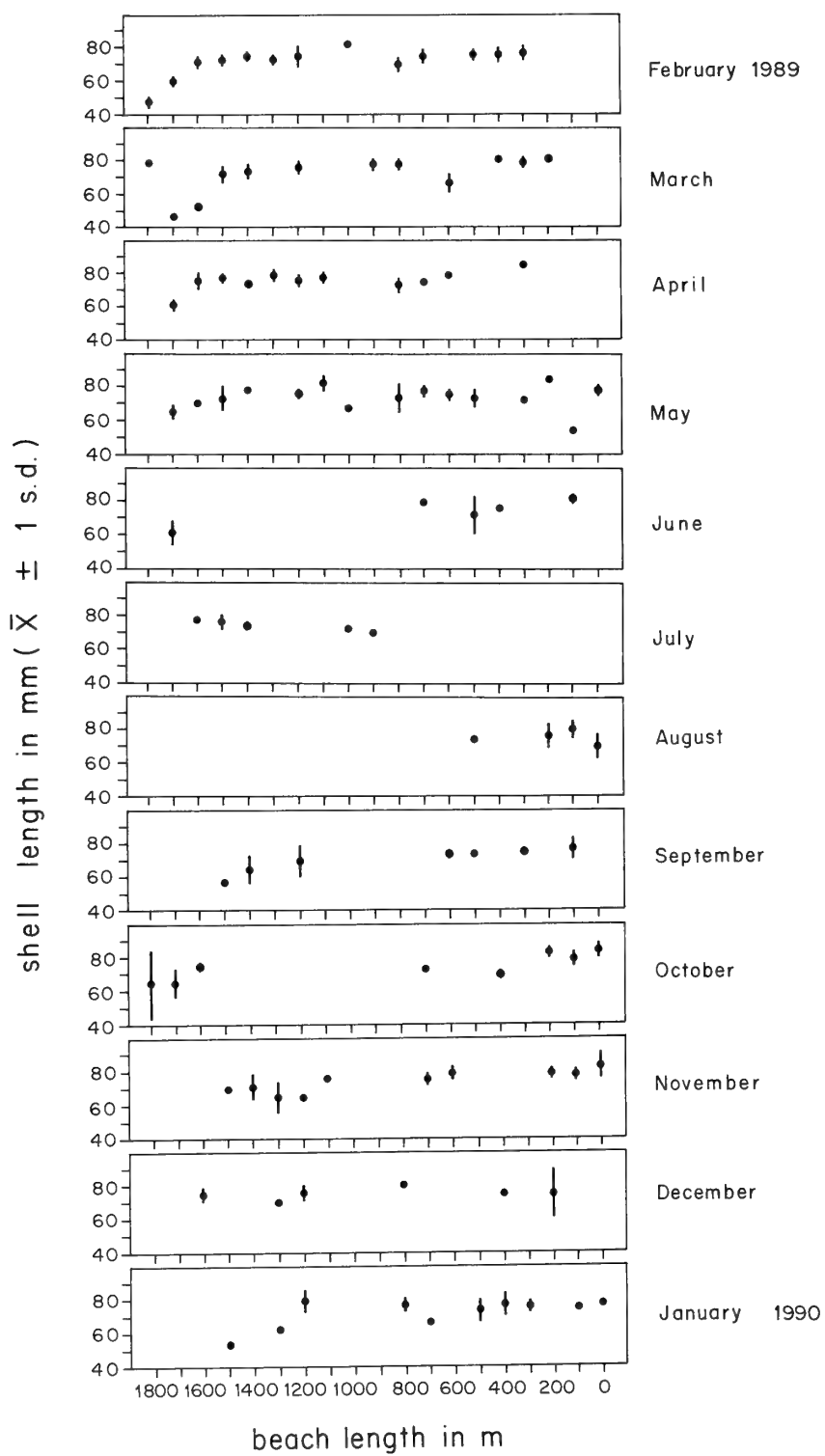


Figure 4

Spatial variability in the mean shell length of *Mesodesma donacium* along the surf zone of the beach at Mehuín.

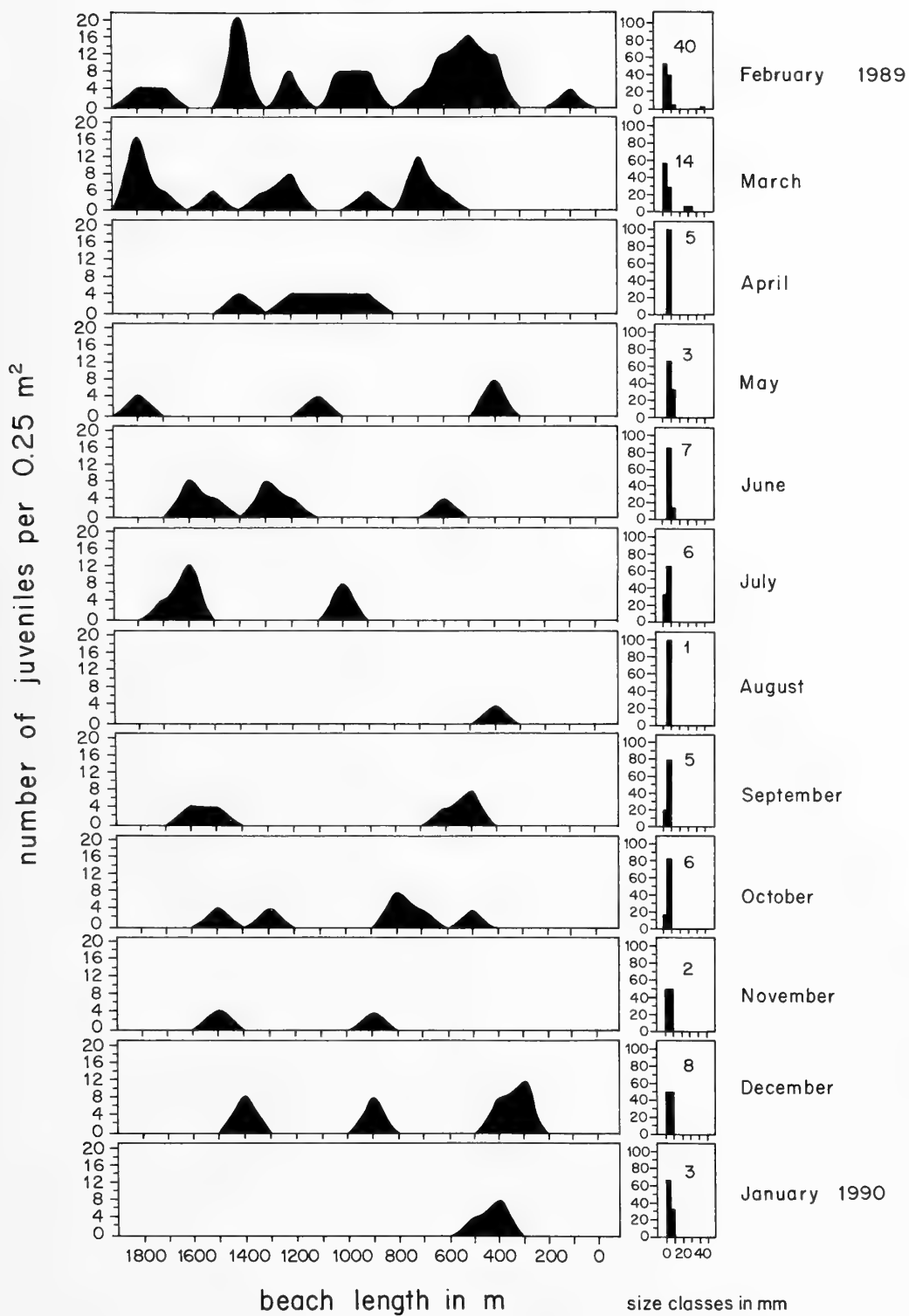


Figure 5

Spatial variability in the density of *Mesodesma donacium* along the swash zone of the beach at Mehuín. The monthly histograms show the size-class distribution (frequency in percentage) of the total number of clams collected each month.

at the final portion of transect A, about 1700–1800 m from the starting point. For example, clams as small as 45–48 mm were collected along the final portion of the transect during February and March (Figure 4). Clams collected in the swash zone (transects B and C) were represented by specimens smaller than 25 mm and also had a discontinuous distribution along the beach (Figure 5). The highest densities of these juvenile specimens (up to 16–20 individuals per 0.25 m²) occurred during February and March.

Monthly values of Morisita's index of dispersion for adult and juvenile clams were significantly greater than 1, indicating an aggregated pattern of distribution (Table 1).

DISCUSSION

The results of this study show that the spatial distribution of *Mesodesma donacium* was patchy. Similar findings were obtained by Tarifeño (1980) for sandy beaches of central Chile and by Defeo et al. (1986) and Olivier et al. (1971) for *M. mactroides* in comparable habitats of Uruguay and Argentina, respectively. *Donax*, another bivalve genus typically inhabiting sandy beaches, also shows an aggregated pattern of distribution, either in warm (Sastre, 1985; Neuberger-Cywiak et al., 1990) or temperate waters (Ansell, 1983; Donn, 1987). The development of a patchy distribution might be related to a high substrate selectivity, as has been shown for *D. denticulatus* (Wade, 1967; Ansell & Trevallion, 1969; Trueman, 1971).

The maintenance of clams in substrates with particular swash or surf characteristics might be related to their burrowing abilities, which in turn are related to grain sizes. For example, Brito & de Mahieu (1981) (not seen but cited in Neuberger-Cywiak et al., 1990) found that the burrowing speed of *Donax denticulatus* was higher in sands with finer grains. Thus, it is quite reasonable to conclude that grain-size characteristics are of primary importance in the distribution of sandy beach clams. However, Sastre (1985) and Neuberger-Cywiak et al. (1990) found that *D. denticulatus* in Puerto Rico and *D. trunculus* in Israel showed aggregated patterns of distribution, in spite of sand-grain sizes being homogeneous along the shore. This agrees with our findings for *Mesodesma donacium* in the beach at Mehuín: thus, causes other than sand-grain size must lead to the patchy distribution of these clams.

Biological interactions have been postulated to produce aggregated distributions in sandy beach organisms. For example, Leber (1982) suggested that the patchy distribution of *Donax* in sandy beaches of North Carolina was related to competition with *Emerita*; however, no strong evidence has been provided to support this suggestion. Predation by birds and fishes has also been invoked as a cause for patchy distribution of sandy beach bivalves (e.g., Loesch, 1957; Wade, 1967; Leber, 1982; Ansell, 1983). Vertebrate predation is not strong enough to affect clam distribution, even when gulls (*Larus dominicanus*) prey on medium-size specimens of *Mesodesma donacium* inhabiting the low levels

Table 1

Values of Morisita's index of dispersion for clams collected in the surf and swash zone of the beach of Mehuín. Values <1 = regular distribution, 1 = random, >1 = aggregated.

Month	Surf zone	Swash zone
February 1989	3.41	2.12
March	2.98	3.01
April	4.69	3.04
May	4.67	6.00
June	1.93	3.53
July	4.40	6.53
August	7.85	17.00
September	4.32	4.37
October	2.61	3.59
November	4.43	7.78
December	4.95	4.06
January 1990	1.91	8.75

of the swash zone. Instead, it is suggested that the temporal variability in the distribution and abundance of *M. donacium* is related to continuous changes in large-scale habitat characteristics.

Short-term changes in beach topography have been documented for the intertidal zone of the beach of Mehuín (Jaramillo, 1987). Similar variability has also been observed for the surf and subtidal zones of this beach; thus, changes in the position of bars, troughs, rip currents and, also, massive transport of sands along the shore occurs over short periods of time (i.e., days and weeks), a situation that may affect the distribution of clams, either by concentrating them in some areas or by causing high mortalities in these populations. This massive transport of sand may also cause emigration to deeper waters, resulting in complete absence or limited abundance of clams in the surf zone during certain months, especially during the winter period. Defeo et al. (1986) mentioned that clam beds of *Mesodesma mactroides* in sandy beaches of Uruguay varied in length day by day as a result of sudden changes in environmental conditions. Neuberger-Cywiak et al. (1990) reported that *Donax trunculus* was more abundant in some shallow underwater rises and suggested that this pattern was produced by active migration and currents. Penchazadeh & Olivier (1975) reported that, in Argentinean sandy beaches, *Donax hanleyanus* had higher abundance in similar rises, while McLachlan & Hesp (1984) found that, in an Australian reflective beach, *Donacilla angusta* and *Donax parva* occurred with the highest abundances in cusp bays, which should provide maximum feeding time. These observations were similar to those of Donn et al. (1986), who found higher abundances of *Donax serra* where beach face slopes were flattest in an intermediate beach in South Africa. This suggests that this bivalve might be able to detect spatial variability in beach slope.

This study has shown a clear size-based separation in the vertical zonation of *Mesodesma donacium*, with the adult

clams restricted to the surf zone and the juveniles primarily in the swash zone. Tarifeño (1980) reported similar findings for sandy beaches in Valparaíso, Chile, trends opposite to those suggested by Arntz et al. (1987) for shallow waters of the Peruvian coast, where many juveniles of *M. donacium* recruit in deeper waters and grow while they migrate toward the shore. The present results are also similar to those for *Donax serra* inhabiting a comparable habitat on the west coast of South Africa, where smaller individuals occur higher in the shore and larger ones farther down (De Villiers, 1975; Donn, 1990). But, in contrast to the findings from the beach at Mehuín, Jaramillo et al. (unpublished data) found that juveniles (in low numbers) coexisted with adults in the surf zone in an intermediate beach near the outlet of the Queule River estuary, 5 km north of Mehuín. Differences in wave disturbance might well account for the local variability in the distribution of juveniles. The more developed breaker zone at the beach of Mehuín could preclude the maintenance of a stable population of juveniles in the surf zone. However, it is also possible that the almost complete absence of juveniles recorded in the surf zone at Mehuín could have been related to the small coring device used in the present study.

Mean shell lengths of adult clams along the surf zone at the beach of Mehuín were similar to those observed in other beaches of Chile (Tarifeño, 1980). Thus, most of these clams probably belonged to the same age class. However, during certain months smaller clams occurred toward the southern section of the longshore sampling transect, close to the outlet of Lingue River estuary. Similar results were reported by Donn (1987), who found that juveniles of *Donax serra* were more abundant toward river mouths in two bays in South Africa. He suggested that spat of *D. serra* were able to select these sheltered areas (Donn, 1987). High abundances of juveniles of *Mesodesma donacium* have also been found in the sand flats located at the mouths of estuaries close to the beach at Mehuín (E. Jaramillo, unpublished data). However, there is insufficient evidence to conclude that this is a similar situation to that suggested by Donn (1987). Extensive sampling in the sublittoral zone of the beach at Mehuín could reveal a similar pattern to that suggested by Arntz et al. (1987) for shallow waters of Peru; that is, considerable recruitment of juveniles.

The present study has shown that the patchy distribution of *Mesodesma donacium* cannot be directly related to changes in sand-grain size characteristics. However, some relationships still may exist, but were not detected because of the span of the sampling schedule. Sudden changes in surf and swash zone morphodynamics should confer changes in textural characteristics of sediments and, if the distribution and abundance of *M. donacium* is related to such large-scale habitat changes, it should also be related to changes in sand-grain size. Clearly, more detailed studies including short-term monitoring of textural and large-scale habitat characteristics are needed to understand the dynamics of surf clam populations in the south of Chile.

ACKNOWLEDGMENTS

We thank Carlos Bertrán, Alejandro Bravo, Sandra Silva, Sonia Fuentealba, Claudio Pavez, Pedro Quijón, Jacqueline Muñoz, Robert Stead, and Victor Poblete for assistance with field work. We acknowledge Dr. Anton McLachlan (University of Port Elizabeth, South Africa) and two anonymous reviewers for suggestions and critical reading of an earlier version of this manuscript. Financial support provided to the senior author by the International Foundation for Science (Sweden) (Grants A/0624-2 and A/0624-3) and Dirección de Investigación y Desarrollo, Universidad Austral de Chile (Project S-90-10) are gratefully appreciated.

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A New Species of *Bolinus* (Gastropoda: Muricidae) from the Caribbean Sea

by

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Abstract. The first species of the genus *Bolinus* Pusch, 1837, from the New World was collected at Isla La Blanquilla, Lesser Antilles, Venezuela. The new species is compared with the type of *Bolinus*, *B. brandaris* (Linnaeus, 1758), from the Mediterranean and *Haustellum chrysostoma* (Sowerby, 1834), a related muricid found off the northern coast of South America. Further comparison is made with *H. mimiwilsoni* Vokes, 1990, and a lot of 13 specimens identified as *H. chrysostoma* from the Plio-Pleistocene Cumaná Formation, Cumaná, Venezuela.

INTRODUCTION

When eight specimens of a muricid species from the southern Caribbean were brought to us, we realized that they were different from any known muricid species. We were unsure of their generic placement since they resembled both *Haustellum* Schumacher, 1817, and *Bolinus* Pusch, 1837. Both genera are described as having a globose body whorl with a long, tubelike canal, a well-developed parietal callus, inductura and rugae on the columellar lip, and no labral tooth. Species in the genus *Haustellum*, as redefined by Ponder & Vokes (1988), have three varices on the body whorl, whereas species of *Bolinus* have five to seven. The eight specimens under study have four to five varices on the body whorl. We have therefore placed the new species in *Bolinus*.

Institutional abbreviations are as follows: LACM, Natural History Museum of Los Angeles County; MNHN, Museum National D'Histoire Naturelle, Paris; SBMNH, Santa Barbara Museum of Natural History; SDNHM, San Diego Museum of Natural History; UCMP, University of California, Museum of Paleontology, Berkeley; USNM, National Museum of Natural History, Smithsonian Institution.

SYSTEMATICS

MURICIDAE Rafinesque, 1815

Bolinus Pusch, 1837

Type species: *Murex brandaris* Linnaeus, 1758, by original designation.

Bolinus hamanni Myers & Hertz, sp. nov.

(Figures 1, 2)

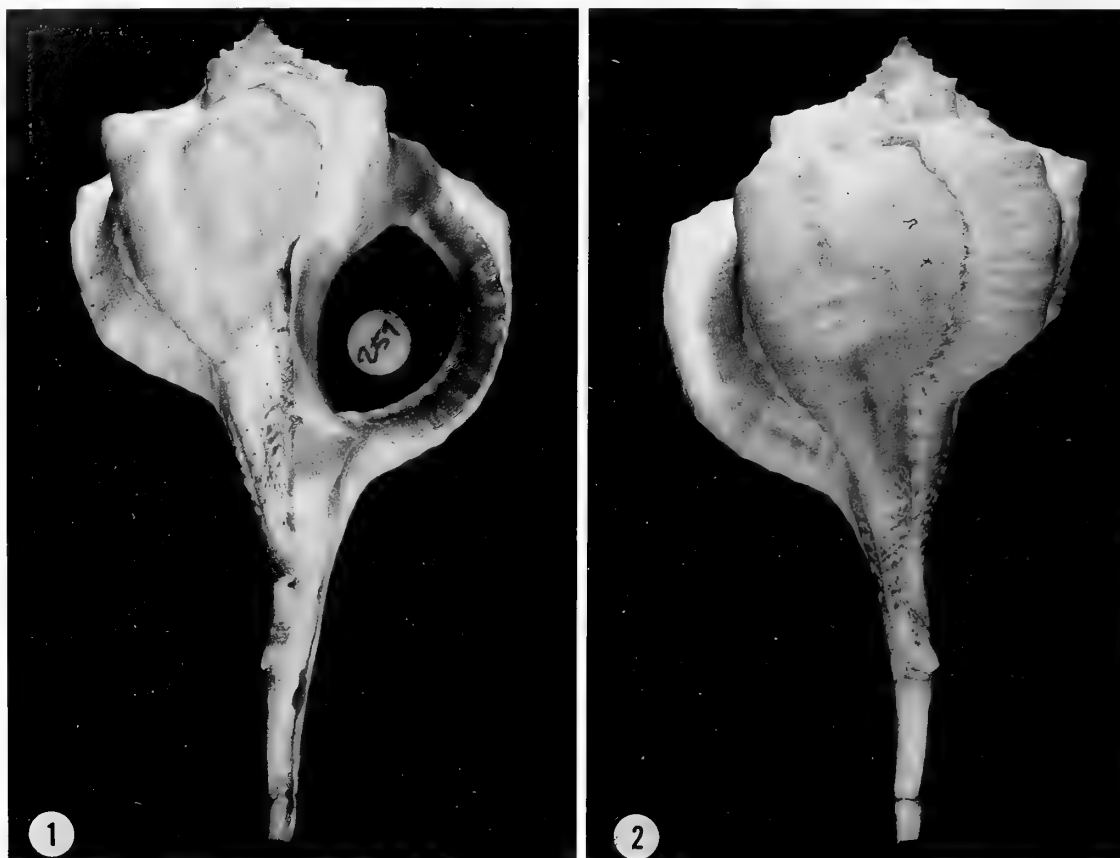
Description: Shell moderately large, heavy, club-shaped; body whorl convex, angulate, broader than high; spire low. Protoconch eroded on holotype. Eight teleoconch whorls; suture irregular, weakly impressed; aperture large, broadly ovate, outer lip thickened, projecting, sharply crenulate reflecting spiral cords; inner surface of outer lip with 16 elongate lirae; columellar lip adherent above expanding to large inductura below, broad shallow anal sulcus separating columella and outer lip; four very faint lirae on columella; entire aperture glossy with cream to deep orange stain. Siphonal canal long, narrowly open, 50% of total shell length, distal end slightly recurved, deflected dorsally and to the right. Body whorl with five thick, rounded varices, developing strong blunt nodes at shoulder; penultimate whorl with four varices. Varices extending from suture across shoulder and terminating midway down siphonal canal; one intervarical node between fourth and fifth varices. Spines lacking. Sixteen weak, irregular spiral cords on body whorl, cords more pronounced on varices. Operculum corneous, unguiculate with five wide concentric ridges, nucleus subterminal. Radula unknown. No soft parts available for study. Shell cream-colored, shading to deep orange on aperture and showing through at leading edge of varices. No periostracum apparent.

Paratype (SBMNH) with partial protoconch of one whorl, smooth, glossy, amber-colored. Two paratypes (SBMNH and MNHN) with four varices; paratype (Ha-

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Figures 1 and 2

Bolinus hamanni Myers & Hertz, sp. nov. Holotype, USNM 860363. Height 101.4 mm, width 53.0 mm. Isla La Blanquilla, Lesser Antilles, Venezuela (11.53°N, 64.38°W) on coarse, clean sand in 18–25 m. Figure 1. Apertural view. Figure 2. Dorsal view.

mann collection) with five varices. All paratypes noded at shoulder and base of body whorl. Paratype (SBMNH) with one node each between second and third and third and fourth varices; paratype (MNHN) with one node each between third and fourth varices and fourth varix and aperture; paratype with immature lip (Hamann collection) with one node each between third and fourth and fourth and fifth varices. Two paratypes (SBMNH and MNHN) with one spine on posterior end of canal and one spine behind inductura; Hamann paratype with spine on posterior end of canal only.

Etymology: It gives us great pleasure to name this species in honor of Gregg Hamann of El Cajon, California, who collected and donated the type specimens.

Type locality: Isla La Blanquilla, Lesser Antilles, Venezuela (11.53°N, 64.38°W) on coarse, clean sand in 18–25 m.

Type material: Holotype USNM 860363, 101.4 mm long, 53.0 mm wide. Paratypes: MNHN, 96.7 mm long, 50.9

mm wide; SBMNH 35649, 94.4 mm long, 54.0 mm wide; Hamann collection, 109.4 mm long, 56.1 mm wide.

Other material studied: Four specimens measuring 100.7 mm long, 52.1 mm wide to 92.8 mm long, 51.6 mm wide, all from the type locality and retained in the collection of Gregg Hamann. Two of the specimens have five varices, and the remaining two specimens have four. The number of lirae on the inner surface of the outer lip varies from 13 to 16, and the number of faint lirae on the columellar lip varies from two to nine. Two of the specimens with five varices have an elongate node abutting the receding side of two varices. All have two spines, one behind the inductura and one on the posterior end of the canal.

Remarks: *Bolinus hamanni* was compared with *Bolinus brandaris* (Linnaeus, 1758), the type of *Bolinus*, and the similar appearing species *Haustellum chrysostoma*, both Recent specimens in the LACM, SDNHM, and Hamann collections, and the Plio-Pleistocene *Haustellum mimiwilsoni* (Vokes, 1990:16, pl. 2, fig. 1) (UCMP 14142) as well as a lot of 13 specimens (UCMP S-110/38646) identified

by Vokes (1990:16, pl. 1, fig. 10) as *H. chrysostoma*, from the Cumaná Formation, Cumaná, Venezuela.

Bolinus hamanni is similar in overall size and shape to *B. brandaris* and has the angulate body whorl, parietal callus and inductura typical of the genus; however, it lacks the strong spines and spiral cords of *B. brandaris* and has four to five varices. *Bolinus brandaris* has five to seven varices.

Bolinus hamanni also resembles *Haustellum chrysostoma*, but is a larger, heavier species attaining a length of 109.4 mm with a low spire compared with the more delicate appearing, higher spired *H. chrysostoma*. *Bolinus hamanni* has four to five thick, rounded varices with faint spiral sculpture, whereas *H. chrysostoma* has three rounded varices, deeply furrowed on the receding side, and spiral sculpture of numerous major and minor cords. *Bolinus hamanni* has occasional intervarical nodes, whereas *H. chrysostoma* has regular, axial intervarical sculpture consisting of a single short ridge, nodose at the shoulder, and weaker costae. *Bolinus hamanni* has four faint lirae on the columellar lip; *H. chrysostoma* has numerous, stronger elongate lirae.

Comparison with the similar appearing Plio-Pleistocene species *H. mimiwilsoni* from the Cumaná Formation, Venezuela, reveals several differences. *Bolinus hamanni* reaches a length of 109 mm with four to five rounded varices and has an irregular, weakly impressed suture and broad anal sulcus. *Haustellum mimiwilsoni* is a 60 mm-long tri-varicate species with a deep channeled suture, having varices greatly excavated on the receding side and lacking an anal sulcus.

Thirteen Plio-Pleistocene specimens, also from the Cumaná Formation, were borrowed from the Museum of Paleontology, University of California, Berkeley (UCMP 38646). This material had been examined by Vokes (1990:16) who noted that there were several specimens of *Haustellum chrysostoma* as well as "several examples that are either gerontic or some sort of ecological variants" (Vokes, 1990:fig. 10). Of the 13 specimens, five have three varices furrowed on the receding side, strong spiral sculpture and intervarical axial sculpture, and eight have four varices on the body whorl not furrowed on the receding side. Vokes

added that the [gerontic] specimens began as normal shells of three varices, but developed the extra varix on the body whorl. We observed that three of the eight also have four varices on the penultimate whorl. All have only occasional intervarical, axial sculpture. One specimen, however, has furrows on the receding side of the first two varices. All the canals are broken. These fossil specimens, if complete, would approach the size of Recent *H. chrysostoma*, but *B. hamanni* is a much larger species which has a body-whorl diameter of 50–56 mm. The body-whorl diameter of the fossil specimens is 30–35 mm. *Bolinus hamanni* has a broad anal sulcus with four very faint lirae on the columella, whereas the fossil specimens have an anal sulcus narrow to lacking and at least 10 strong rugae on the columella.

ACKNOWLEDGMENTS

We wish to thank D. R. Lindberg of the University of California Museum of Paleontology, Berkeley, and J. H. McLean of the Natural History Museum of Los Angeles County for the loan of specimens from their institutions. We are grateful to the San Diego Natural History Museum for making their facilities, library, and collection available to us. We thank Gregg Hamann of El Cajon, California, for bringing the specimens to our attention and donating the three type specimens. We further appreciate the fine photographs of the holotype by D. K. Mulliner. E. H. Vokes and A. D'Attilio kindly read the manuscript and gave encouragement and constructive comments.

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On the *Conus jaspideus* Complex of the Western Atlantic (Gastropoda: Conidae)

by

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Abstract. Synonyms, type specimens, type localities, shell redescrptions, external anatomy, habitat, geographic distribution, and fossil records are presented for the gastropod mollusks *Conus jaspideus*, *C. mindanus*, and *C. pusio*. For the first time, the taxonomy of this species group is based on anatomical characters. The three species are placed in a complex of sibling species because they are morphologically similar, except for differences in the anatomy and position at rest of the genitalia. To respect chronological order, the complex is named after the first described taxon, *C. jaspideus*.

INTRODUCTION

The original diagnosis and subdescription of *Conus jaspideus* Gmelin, 1791, was insufficient to identify any species of *Conus* in the Western Atlantic. Clench (1942) re-described *C. jaspideus*, designated a lectotype, and considered *C. pusio* Hwass in Bruguière, 1792, as a junior synonym. *C. jaspideus*, of the western Atlantic, as re-described by Clench (1942), was considered as a valid species by Kohn (1966) in the interest of stability of zoological nomenclature.

Conus mindanus Hwass in Bruguière, 1792, was described as a species from the Philippines. Lamarck (1822) maintained the original locality, and Weinkauff (1875) commented on the occurrence of *C. mindanus* in the Antilles, and mentioned that it did not occur in the eastern India region. The holotype label of *C. mindanus* in the Lamarck Collection (Muséum d'Histoire naturelle de Genève) is marked "Localité Philip."; living specimens of this species have never since been found in the Indo-Pacific region. Many specimens of *C. mindanus* have been illustrated as *C. jaspideus* by authors studying the western Atlantic fauna. Kohn (1968) noted that a study then in progress (by Van Mol & Tursch) indicated that *C. mindanus* may intergrade with *C. jaspideus*.

Conus pusio was described by Hwass in Bruguière (1792) as a Caribbean species and was considered a junior synonym of *C. jaspideus* not only by Clench (1942), but also by Abbott (1958, 1974), Van Mol et al. (1967), and Kohn (1968). Costa (1990) studied the behavior and life habits of *C. pusio*, misnamed as *C. jaspideus*, on the basis of shell characters and literature available at the time.

Vink (1989, 1991), agreeing with the original descriptions, maintained *Conus jaspideus*, *C. mindanus*, and *C.*

pusio as three distinct species and furnished an extensive synonym list for each one.

For two centuries following the original descriptions of *Conus jaspideus*, *C. mindanus*, and *C. pusio*, authors' opinions on the validity of the three taxa, expressed both in scientific and popular literature, were based only on shell characters. This reliance did not adequately reveal the true identity of the species. Herein the taxonomy of this species group is based on anatomical characters presented for the first time. This study also proposes a complex of sibling species as defined by Mayr (1942). *Conus jaspideus*, *C. mindanus*, and *C. pusio* exhibit a similar shell with some morphs of difficult placement, but differences in penis anatomy and its rest position are evident.

MATERIALS AND METHODS

The material on which this study was based is deposited in the Collections of the Muséum d'Histoire naturelle de Genève (MHNG), the Institut Royal des Sciences Naturelles de Belgique (IRSNB), the Zoologisch Museum, Universiteit Van Amsterdam (ZMA), the Florida Museum of Natural History (FMNH), and the author (FHAC). Observations of external anatomy were based on specimens collected from the coasts of Florida (USA), Bahia, Espírito Santo, and Rio de Janeiro (Brazil).

The specimens were collected in the intertidal zone at low tide, in the subtidal zone by skin and SCUBA dives, and on the Continental Shelf by dredges and shrimp nets. Animals were narcotized in low temperatures of 5°C to 6°C, immersed in seawater for a period of 24 to 48 hours, and preserved in 70% ethanol. Data concerning habitat and bathymetric distribution were based only on animals collected or observed alive.

Table 1
Summary of a comparison between *Conus jaspideus*, *C. mindanus*, and *C. pusio*.

	<i>C. jaspideus</i>	<i>C. mindanus</i>	<i>C. pusio</i>
Shell			
Zone between protoconch and teleoconch	conspicuous growth lines, formation of a carina	conspicuous axial costae	inconspicuous growth lines
Shoulder of the first teleoconch whorls	carinated (may be angular or rounded in adults)	angular (remains in adults)	rounded (remains in adults)
Soft parts			
Penis			
Rest position	bent upward and lodged inside pallial cavity	bent backward, forward or hanging down	bent backward, below the mantle margin
Anatomy	basal fold, sharp extremity	grooved base, rhomboidal extremity	basal fold, long ventral groove and distal filament
Geographical distribution			
Sympatry	Caribbean Sea and Brazil Florida	Caribbean Sea and Brazil Florida	Caribbean Sea and Brazil —
Allopatry	Gulf of Mexico	Bermuda	—
Bathymetric distribution in meters (only live specimens)	0.0 to 51.0	0.0 to 153.0	0.0 to 23.0
Fossil records	Pliocene and Pleistocene	not known	not known

Shells were broken and fragments removed to expose the soft bodies. Subsequently, specimens were immersed in a solution (1%) of toluidine blue in distilled water and drawn with the aid of a camera lucida. The external anatomy of 10 males of each species was examined.

Shell drawings, which have been missing from previous reports, were also made with a camera lucida. These drawings are preferred over photographs because drawings show details of form that in photographs are frequently hidden by variations in color patterns.

The synonym lists include only those species for which type material or original descriptions could be related to specimens whose soft parts were studied. A summary comparing the three species studied herein is presented in Table 1.

RESULTS

Conus jaspideus Gmelin, 1791

(Figures 1–4)

Conus jaspideus Gmelin, 1791, p. 3387.

Conus verrucosus Hwass in Bruguière, 1792, p. 708.

Conus pealii Green, 1830, p. 123, pl. 3, fig. 3.

Conus stearnsii Conrad, 1869, p. 104, pl. 10, fig. 1.

Type: Fig. 612, plate 55 in Martini (1773), was selected by Clench (1942) as lectotype. Topotypes are in FMNH No. 63315.

Type locality: Puerto Plata, Dominican Republic, designated by Clench (1942).

Redescription: Shell small for the genus; in 62 specimens with protoconch, average length by number of whorls 20.1 mm/9.3, reaching maximum of 28.6 mm/11.0. Color white, light gray, beige, orange, pink, or brown with axial and/or spiral flammules or streaks of orange, purple, or brown. Spire high, about one-third of shell length, and stepped in outline. Earlier teleoconch whorls concave or flat above the carinated shoulder, characters that may disappear in later whorls. Aperture oblique, slightly wider near base, outer lip thin and smooth inside, columella hidden. Body whorl slightly convex to flat-sided, with spiral grooves near base that become obsolete or absent near shoulder. Shell marked by sub-microscopic axial threads curved over shoulder. Some specimens with granulated shells; in total of 630 examined, 486 (77.1%) were smooth, 102 (16.1%) granulated, and 42 (6.7%) intergraded. Periostracum smooth, transparent light beige.

Protoconch mamillate, globose and smooth, of paucispiral type with 1.5 to 2.0 whorls, white, beige, pink, or purple, translucent, limited by a stage of conspicuous growth lines.

External anatomy: Animal whitish with black mottling around foot, on head and siphon, and with diffuse pigmentation on roof of pallial cavity. Operculum horny, small, oval or unguiculate.

The penis, originating behind the head at the right side, is long, laterally compressed, with a basal fold and a distal sharp extremity with a depression on its lower side. It rests bent upward and lodged inside the pallial cavity.

Habitat: Sand, sand with broken shells and coral slabs,

sand with algae, sand with mud, broken shells, coral, mud, rock, rock with a layer of sand or mud, between 0.0 mm and 51.0 m depth.

Geographical distribution: Florida, Gulf of Mexico, Caribbean Sea, and Brazil.

Fossil records: Reported and illustrated under the name of *Conus* cf. *verrucosus* to Mexico Pliocene by Böse (1906) based on one shell fragment, the age of which was attributed to Miocene by Perrilliat (1974), to Florida Pliocene by Smith (1930) and Sage (1990). *C. jaspideus* is well-represented by fossils from Plio-Pleistocene and Pleistocene in the collection of FMNH.

Conus mindanus Hwass in Bruguière, 1792

(Figures 5–8)

Conus mindanus Hwass in Bruguière, 1792, p. 711.

Conus agassizii Dall, 1885/1886, pl. 9, fig. 8.

Conus agassizii Dall, 1889, p. 68.

Conus bermudensis Clench, 1942, p. 34, pl. 13, fig. 4.

Conus bermudensis lymani Clench, 1942, p. 35, pl. 13, fig. 3.

Conus iansa Petuch, 1979, p. 542, fig. 4 G, H.

Type: The holotype is in the Lamarck Collection No. 122, in MHNG No. 1107/16.

Type locality: The locality cited in the original description as the Philippines by Hwass in Bruguière (1792) was considered erroneous by Weinkauff (1875), Kohn (1968), and Vink (1989). Following Recommendation 72H(b) of the International Code of Zoological Nomenclature (1985), the type locality of *Conus mindanus* is herein corrected to 46.0 m depth in north of Nellies Point, South Lake Worth, Palm Beach Co., Florida, USA. This is the same locality as that of the holotype of *C. bermudensis lymani* (= *C. mindanus*) in FMNH No. 13362, and the choice for the same type locality is justified due to strong similarities between the two holotypes.

Redescription: Shell medium for the genus, in 38 specimens with protoconch, average length by number of whorls 25.6 mm/9.1, reaching maximum of 44.6 mm/10.0. Color white, beige, pink, or brown with axial flammules or streaks that may be arranged in two spiral zones of yellow, pink, or brown. Some specimens have spiral white rows with brown rectangular dots. Spire medium, about one-fourth of shell length, straight-sided or stepped in outline. Earlier teleoconch whorls concave above angular shoulder, characters that remain in later whorls. Aperture oblique, slightly wider near base, outer lip thin and smooth inside, columella exposed near base. Body whorl slightly convex, with spiral grooves near base that disappear or are replaced by spiral threads near shoulder. Shell marked by sub-microscopic axial threads curved over shoulder. Some specimens with granulated shells, in total of 162 examined, 131 (80.8%) were smooth, 23 (14.2%) granulated, and 8 (4.9%) intergraded. Periostracum with axial striae, transparent and light beige.

Protoconch mamillate, globose and smooth, of paucispi-

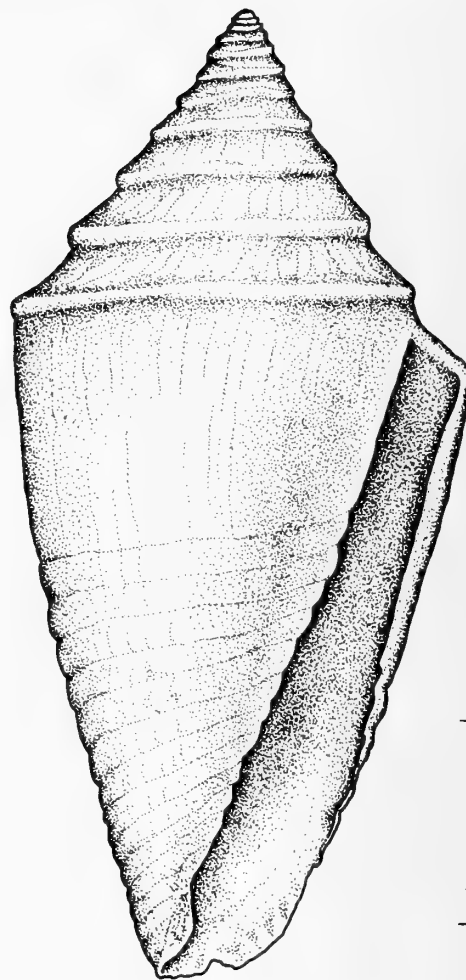


Figure 1

Shell of *Conus jaspideus*, Sanibel Island, Florida, scale bar 5.0 mm (FHAC).

ral type with 2.0 whorls, yellowish or pinkish, opaque, limited by a conspicuous axial costae.

External anatomy: Animal beige with black mottling around foot and on head. Siphon with vertical black stripes. Operculum horny, small, oval or unguiculate.

The penis, originating behind the head at the right side, is long, laterally compressed, with a narrow and vertically grooved basal third and a distal rhomboidal extremity with a concave inferior outline. It rests bent backward, forward or, hanging down, lodged between the foot and the inner side of outer lip of the shell.

Habitat: Sand, sand with rock and coral slabs, broken shells, mud, between 0.0 m and 153.0 m depth.

Geographical distribution: Bermuda, Florida, Caribbean Sea, and Brazil.

Fossil records: Fossils of this species are not presently known.

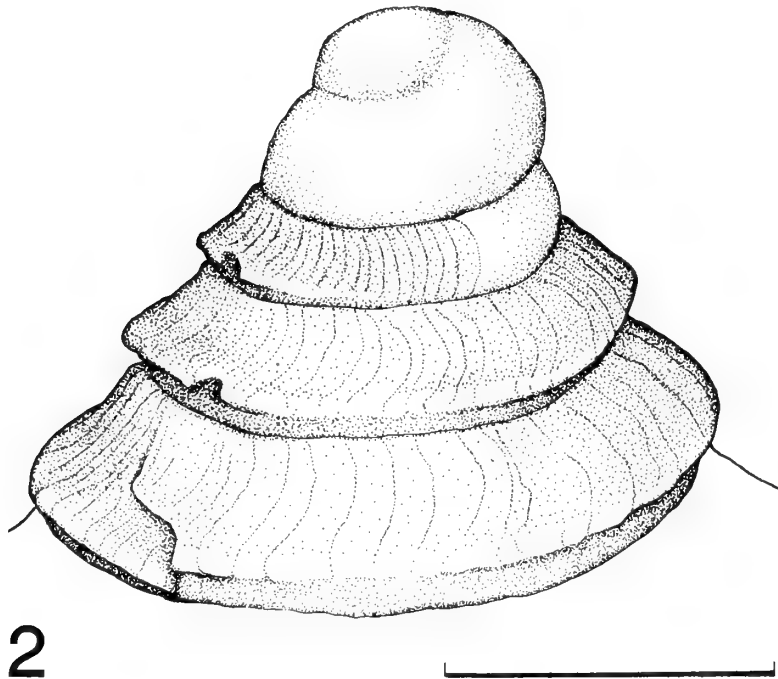


Figure 2

Protoconch and first teleoconch whorls of *Conus jaspideus*, off Rio Maroni, French Guiana, scale bar 1.0 mm (FMNH).

Conus pusio Hwass in Bruguière, 1792
(Figures 9–12)

Conus pusio Hwass in Bruguière, 1792, p. 710.

Conus pusillus Lamarck, 1810, p. 39.

Conus duvali Bernardi, 1862, p. 404, pl. 13, fig. 3.

Type: Fig. 4, plate 334 in Lamarck (1816) was designated by Kohn (1968) as holotype.

Type locality: Kohn (1968) selected Santo Domingo as the type locality, the first locality noted in the original description: “à Saint-Domingue, à la Martinique et à la Guadeloupe” (Hwass in Bruguière, 1792).

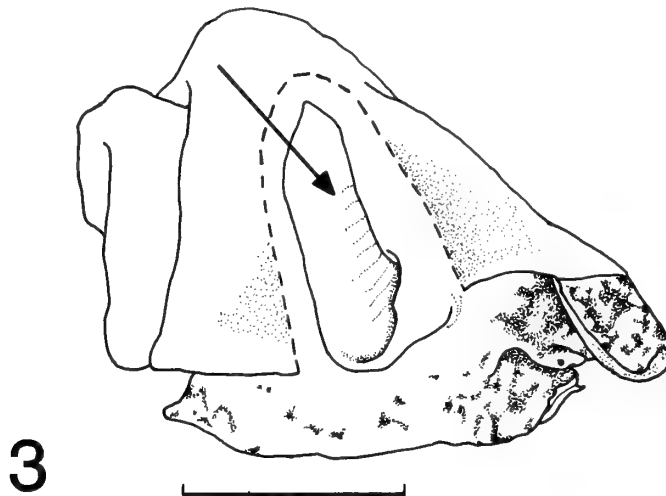


Figure 3

Right side of a male specimen of *Conus jaspideus* removed from shell, showing the penis (arrow), scale bar 3.0 mm. Mantle removed at the dashed line for clarity.

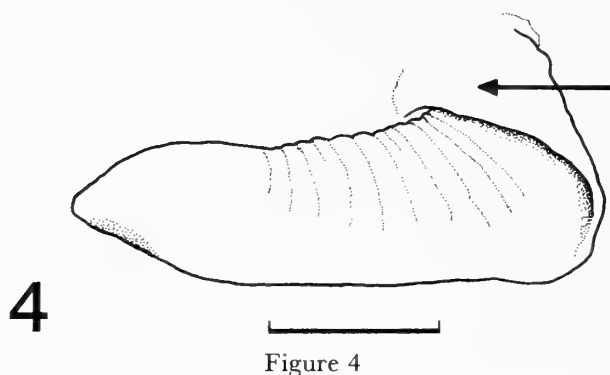


Figure 4

Penis of *Conus jaspideus*, showing the basal fold (arrow), scale bar 1.0 mm.

Redescription: Shell small for the genus, in 21 specimens with protoconch, average length by number of whorls 18.7 mm/7.3, reaching maximum of 24.5 mm/9.0. Color beige, orange, pink, or purple with axial flammules of white or brown; some specimens have spiral white rows with brown arrowhead marks. Spire medium to high, between one-fourth to one-third of shell length and straight-sided in outline. Earlier teleoconch whorls flat above rounded shoulder, characters that remain in later whorls. Aperture oblique, slightly wider near base, outer lip thin and crenulated inside in full-grown specimens. Columella partially exposed near base. Body whorl slightly convex, with spiral grooves near base that disappear or are replaced by spiral threads near shoulder. Shell marked by sub-microscopic axial threads curved over shoulder. Some specimens with granulated shells, in total of 497 examined, 484 (97.3%) were smooth, 6 (1.2%) granulated, and 7 (1.4%) intergraded. Periostracum smooth, translucent light gray.

Protoconch mamillate, globose and smooth, of paucispiral type with 2.0 to 2.5 whorls, white, beige, or light brown, opaque, limited by a formation of inconspicuous growth lines on teleoconch surface.

External anatomy: Animal beige with black mottling around foot, on head and siphon. Outer margin of mantle highlighted by brown band from which perpendicular stripes originate. Operculum horny, oval or unguiculate.

The penis, originating behind the head at the right side, is long, laterally compressed, with a basal fold, a ventral groove on its last two-thirds, and a conspicuous distal filament. It rests bent backward below the margin of the mantle, lodged between the foot and the inner side of the outer lip of the shell.

Habitat: Sand, sand with broken shells and coral slabs, broken shells, rock with a layer of sand or mud, between 0.0 m and 23.0 m depth. For behavior and life habits of *Conus pusio* see Costa (1990), under the name of *C. jaspideus*.

Geographical distributions: Caribbean Sea and Brazil.

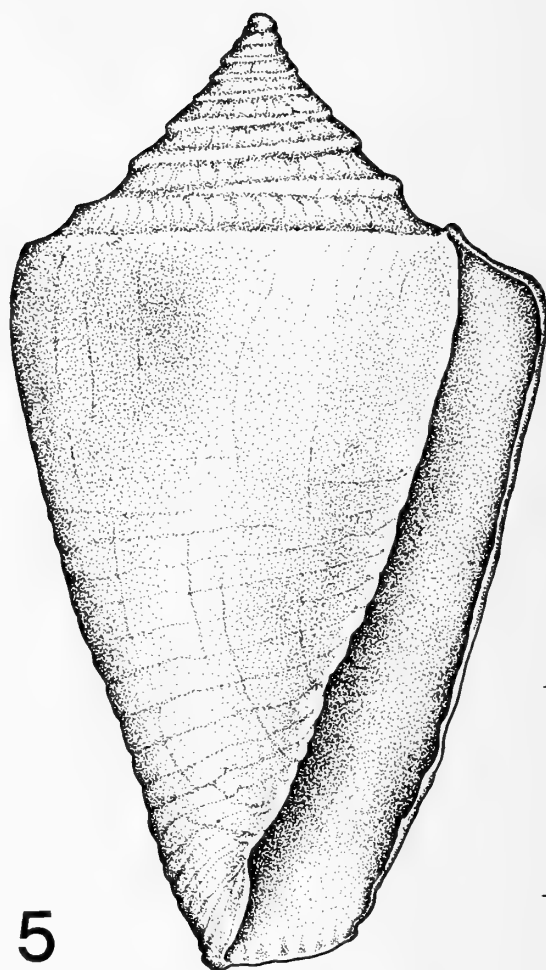


Figure 5

Shell of *Conus mindanus*, Cabo Frio, Rio de Janeiro State, scale bar 5.0 mm (FHAC).

Fossil records: Fossils of this species are not presently known.

DISCUSSION

Vink (1989) attempted to correct the type locality of *Conus pusio* to Guadeloupe, on the basis that specimens from Santo Domingo were unknown to him. Vink (1991) also attempted to correct the type locality of *C. jaspideus* to Monos Island, Trinidad. Since both *C. jaspideus* and *C. pusio* occur in the Dominican Republic, the previously designated type localities of *C. jaspideus* in Puerto Plata by Clench (1942) and of *C. pusio* in Santo Domingo by Kohn (1968) are within the geographic range of those taxa. Consequently, they are in agreement with Recommendation 72H(a) (4) of the International Code of Zoological Nomenclature (1985) and should be maintained. The attempts of Vink (1989, 1991) in correcting these type lo-

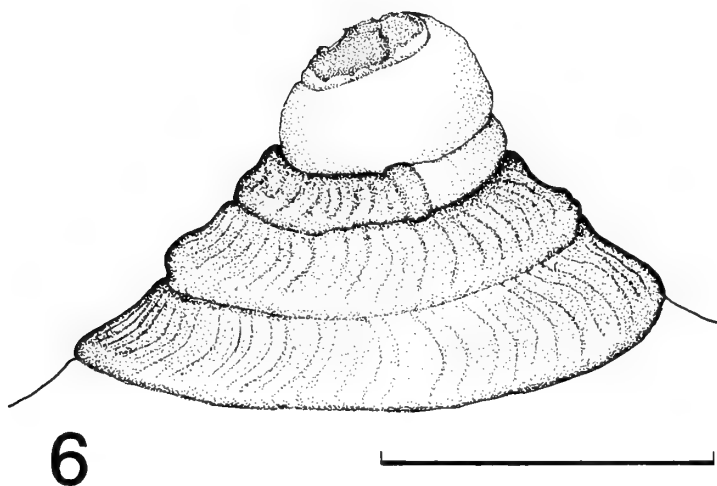


Figure 6

Protoconch and first teleoconch whorls of *Conus mindanus*, off Bermuda Island, scale bar 1.0 mm (FMNH).

calities conflict with Recommendations 72(a) and (b) of the International Code of Zoological Nomenclature (1985) and thus should be regarded as invalid.

Coomans (1973) noted the scarcity of sculpture on cone shells, but some species had two phenotypic variations: smooth and granulated. Coomans (1973) also pointed out that different ecological conditions could not be proven to cause granulated shells, and suggested a genetic origin.

Abbott (1958) observed in Grand Cayman Island that shells of *Conus jaspideus* with the granulated pattern pre-

dominate in coralline, turbulent environments, while smooth shells were more abundant in protected sand shores.

Comparisons between series of *Conus jaspideus* shells from Salvador, Bahia, Brazil, and Puerto Plata, Dominican Republic, showed that juveniles from the two localities are similar enough not to be correlated with geographic area. The adults from Puerto Plata have more developed granules and darker colors than those from Salvador, probably the result of environmental influences during shell growth.

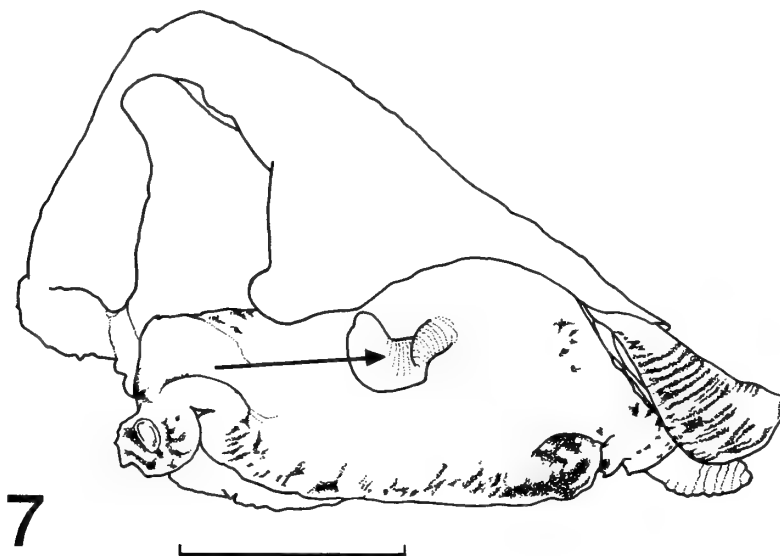


Figure 7

Right side of a male specimen of *Conus mindanus* removed from shell, showing the penis (arrow), scale bar 4.0 mm.



Figure 8

Penis of *Conus mindanus*, showing the narrow basal third (arrow), scale bar 1.0 mm.

The smooth pattern is more common and evidently dominant over the granulated pattern in *Conus jaspideus*, *C. mindanus*, and *C. pusio*. But for all three species, smooth, granulated, and intergraded forms can be found among specimens living at the same locality.

Mayr (1942) defined sibling species as sympatric forms that are morphologically very similar or indistinguishable, have specific biological characteristics, and are reproductive isolates. *Conus jaspideus*, *C. mindanus*, and *C. pusio* have shell and animal colorations with many similarities and overlapping geographical distributions. Although their bathymetric distributions are different, the three species can be found living together at the same floor in determined areas. There are anatomical differences in the penis, and also in its rest position, that may offer a physical or mechanical barrier for copulation with a consequent reproductive isolation between *C. jaspideus*, *C. mindanus*, and *C. pusio*. Thus, the three species studied herein are placed in a complex of sibling species that is named after the first described taxon, *C. jaspideus*.

Chaney (1987) pointed out that *Conus mahogani* Reeve, 1843, and *C. ximenes* Gray, 1839, from the Panamic Province share an identical radula and the same body coloration. Chaney (1987) also stated that there are color differences in the shell and that these two species could easily be separated by the external anatomy of the cephalic penis. The species studied by Chaney (1987) should also be considered sibling species.

Fossil shells from the Pliocene of Mexico were misdescribed as a variety of *Conus agassizii* Dall, 1885 (= *C. mindanus*) of recent fauna, and named *C. agassizi* [sic] Dall, var. *multiliratus* Böse, 1906. In his comments, Böse (1906) pointed out that his fossil shells were similar to juveniles of *C. agassizii* but distinct from adults of this species. Costa (1988, 1992, and herein) pointed out that juvenile shells

of *Conus* can be different from adults, and the length of the shells indicated by Böse (1906) ranged between 20 mm and 28.5 mm, which is large for juveniles of *C. agassizii* (= *C. mindanus*). Also, the high-spined and stubbed shells, with strong rounded spiral threads and deep grooves all over the body whorl, described and illustrated by Böse

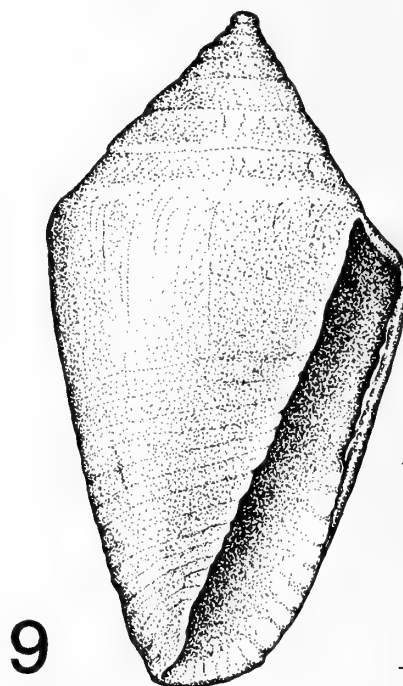


Figure 9

Shell of *Conus pusio*, Cabo Frio, Rio de Janeiro State, scale bar 5.0 mm (FHAC).

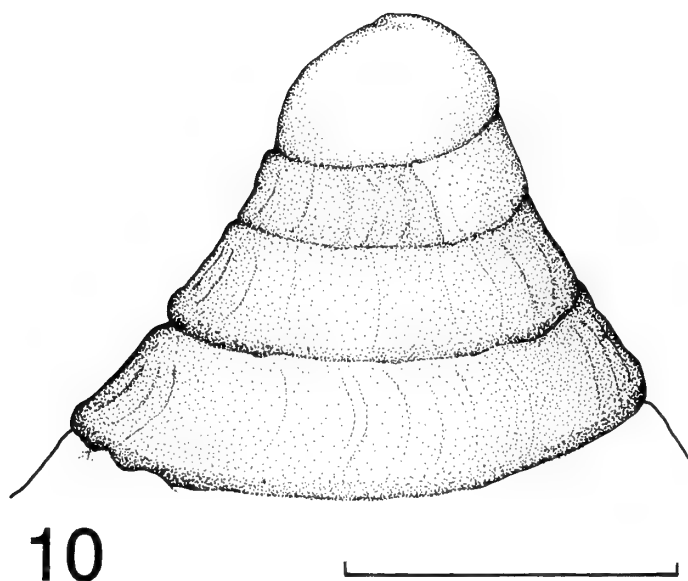


Figure 10

Protoconch and first teleoconch whorls of *Conus pusio*, Cabo Frio, Rio de Janeiro State, scale bar 1.0 mm (FHAC).

(1906), are related to the recent *C. austini* Rehder & Abbott, 1951 from Florida, Mexico, Caribbean Sea, and Brazil, and hold few affinities with *C. agassizii* (= *C. mindanus*) adults. Perriliat (1974) attributed to Miocene the age of *C. agassizi* Dall, var. *multiliratus*. The shells described by Böse (1906), and alleged to be a variety of *C. agassizii*, in fact warrant the rank of species and should be named *C. multiliratus* (Böse, 1906). Fossils of *C. agassizii* s.s., both juveniles and adults, are still unknown.

Sutty (1984) commented on the occurrence of fossils of *Conus mindanus* without recording locality, formation, age, depository collection, or an illustration, which makes the information unreliable.

The fossil records of *Conus jaspideus caboblanquensis* Weisbord, 1962, from the Pleistocene of Venezuela should be regarded as *C. puncticulatus* Hwass in Bruguière, 1792, because the shell characters and illustrations presented by Weisbord (1962) are similar to recent specimens of *C.*

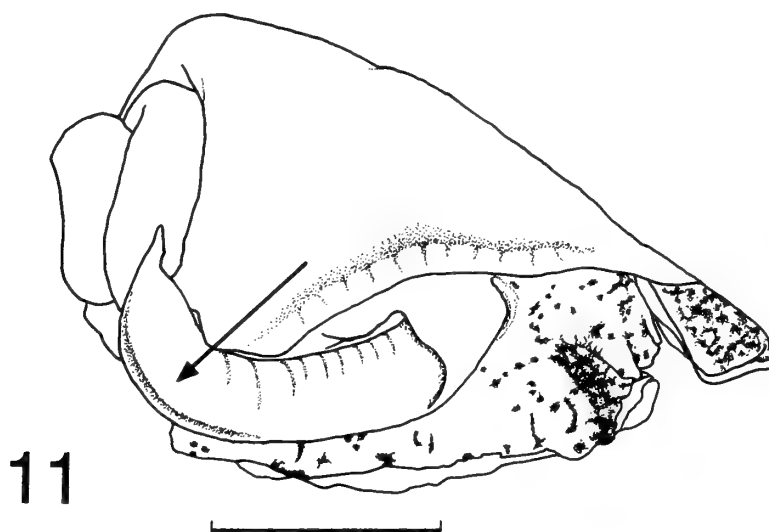


Figure 11

Right side of a male specimen of *Conus pusio* removed from shell, showing the penis (arrow), scale bar 4.0 mm.

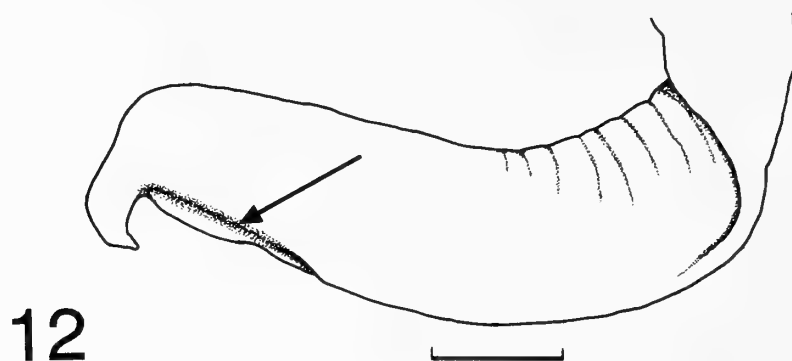


Figure 12

Penis of *Conus pusio*, showing part of the ventral groove (arrow), scale bar 1.0 mm.

puncticulatus from Panama, Venezuela, Aruba, Martinique, and Tobago but not to *C. jaspideus*.

ACKNOWLEDGMENTS

I am indebted to Dr. Walter Narchi, University of São Paulo, for his suggestions and criticisms while this study was being developed. To Dr. Yves Finet, Muséum d'Histoire naturelle de Genève, Dr. Henry E. Coomans, Zoologisch Museum, Universiteit Van Amsterdam, Drs. Fred Thompson, Kurt Auffenberg, and Douglas S. Jones, Florida Museum of Natural History, for allowing access to the specimens in the above mentioned institutions. To Edward Wils for access to his collection, deposited in the Institut Royal des Sciences Naturelles de Belgique.

I thank Drs. Alan J. Kohn, Matthew J. James, James Nybakken, Walter Sage, Eliézer de C. Rios, Fábio Moritzsohn, Henry W. Chaney, and Danker L. N. Vink for supplying literature.

I also wish to acknowledge the divers Giovani Costa Martins and Leonora Fritzsche for support during underwater fieldwork.

Special thanks to Diane Burger-Costa for illustration of the shells and revision of the original text.

This study was developed at the University of São Paulo, Brazil, and partially supported by a scholarship from CAPES and a grant from Conchologists of America.

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NOTES, INFORMATION & NEWS

Diet and Mode of Feeding of the Muricid Gastropod *Acanthinucella lugubris angelica* in the Northern Gulf of California

by

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Edith Zipser¹ and Hermine E. Vermeij³

One of the most characteristic predatory gastropods of the middle and upper intertidal zone in the northern Gulf of California is the muricid *Acanthinucella lugubris angelica* (Oldroyd, 1918). This species, which has usually been called *Acanthina angelica* in the ecological literature, belongs to the distinctive ocenebrine genus *Acanthinucella* (Cooke, 1918), which has existed in the temperate and subtropical northeastern Pacific since latest Oligocene or earliest Miocene time (see Wu, 1985, for species-level taxonomy; and Vermeij, 1993, for generic assignment). Earlier observations (Paine, 1966a, b; Malusa, 1985; Lively, 1986; Lively & Raimondi, 1987; Lively et al., 1993) have implied that *A. l. angelica* is a trophic specialist whose diet consists entirely of the barnacles *Chthamalus anisopoma* Pilsbry, 1916, and *Tetracita stalactifera* Lamarck, 1818. The well-developed labral spine, a ventrally directed projection near the anterior end of the outer lip of the shell, has been shown to aid in feeding on barnacles. It enables the predator to wedge open or to break the opercular plates of prey barnacles, so that the latter are attacked by way of the aperture rather than by drilling through the opercular or lateral plates (Paine, 1966b; Hemingway, 1975; Sleder, 1981; Malusa, 1985; Perry, 1985; Lively, 1986). The apparently restricted diet of *A. l. angelica* has been interpreted as an example of trophic specialization by a species in a complex food web in which several predatory species must divide up the prey resource (Paine, 1966a).

As part of a larger study by one of us (G.J.V.) on the evolution of labral spines in gastropods, we observed *A. l. angelica* feeding at several sites in the vicinity of Puerto Peñasco, Sonora, Mexico, in the northern Gulf of California. One of us (H.E.V.) saw *A. l. angelica* eating small mussels, which were apparently opened with the use of the labral spine. This showed that *A. l. angelica* is not a barnacle specialist. H. Vermeij's observations prompted us to document the mode of feeding and diet of *A. l. angelica*. Here we report these findings, and comment on patterns

of dietary specialization and their consequences for the interpretation of intertidal food webs.

We observed *A. l. angelica* on rising tides following early morning low water during March, 1993. Lively & Raimondi (1987) had previously demonstrated that this predator feeds while the tide is out. The food and position of each snail were carefully examined at each of three sites in the vicinity of Puerto Peñasco (Table 1). We observed that feeding snails clung tightly to the rock, whereas resting snails were weakly attached and were easily dislodged.

Acanthinucella lugubris angelica had a fairly broad diet consisting of one barnacle, one gastropod, and three bivalve species, all with sessile life habits (Table 1). We also noted feeding on the barnacle *Chthamalus anisopoma*, but did not include these instances because our survey was made on snails above the zone occupied by this barnacle. Previous authors have, however, amply demonstrated that *A. l. angelica* feeds on *Chthamalus*, and that the latter species is capable of responding phenotypically to the predator by growing so as to orient the aperture laterally rather than upward (see Lively, 1986).

Although the data imply that barnacles constitute the majority of prey at two of the three sites (Playa Las Conchas and Punta Pelicano), other prey may nonetheless be important. As Fairweather & Underwood (1983) and Kent (1983) have pointed out, prey that require long handling times for subjugation and consumption are overrepresented in field surveys of predation, whereas species that can be dealt with rapidly by the predator are underrepresented. Small prey, such as the mussel *Brachidontes semilaevis*, are thus less likely to be observed being consumed than is the large barnacle *Tetracita stalactifera* or the oyster *Saccostrea palmula*.

Our data suggest further that the diet and method of feeding of *A. l. angelica* vary from place to place. At Playa Las Conchas, most *Tetracita* (30 of 45 individuals, 67%) were attacked by way of the aperture; the labral spine was positioned directly over the barnacle's aperture, and there was no sign of drilling. At Punta Pelicano, on the other hand, *Tetracita* was taken mainly by drilling through the lateral plates (15 of 22 observations, 68%). Mussels (*Brachidontes semilaevis*) at Playa las Conchas were attacked at the posterodorsal margin. Almost no overlap in diet existed between Bahia Cholla, where all individuals of *A. l. angelica* were observed to be drilling through the upper valves of the oyster *Saccostrea palmula*, and the other two sites. These observations reinforce Paine's (1980) important point that the ecological role of predators varies greatly among sites, and that studies confined to single sites or to short durations may be misleading.

Our findings contribute to a growing body of evidence that few, if any, predatory gastropods are dietary special-

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Table 1

Prey species and mode of feeding of *Acanthinucella lugubris angelica* at three sites in the vicinity of Puerto Peñasco, Sonora.

Site and prey species	Observations	Number drilled
Playa Las Conchas		
<i>Tetraclita stalactifera</i> Lamarck, 1818	45	15
<i>Brachidontes semilaevis</i> (Menke, 1849)	10	0
<i>Isognomon quadratus</i> (Anton, 1837)	1	0
<i>Saccostrea palmula</i> (Carpenter, 1857)	1	1
Vermetidae	2	0
Punta Pelicano		
<i>Tetraclita stalactifera</i>	22	15
Bahia Cholla		
<i>Saccostrea palmula</i>	11	11

ists. Many predatory gastropods may be restricted to a particular functional category of prey such as sedentary suspension-feeders (as in the case of *A. l. angelica*) or mobile prey, but within such categories they eat a variety of prey species. Ecological links involving predatory gastropods are therefore among groups of species; that is, no one species is strictly dependent on any other in the food web. This circumstance makes strict coevolution—the reciprocal response of species to evolutionary changes in each other—unlikely, and also provides a measure of flexibility in the way food webs are organized. Although dietary breadth of predatory gastropods may be generally less in communities composed of many species than in those where only a few predatory species divide up the prey resource (Kohn, 1966, 1978; Taylor, 1976), we believe that the extent of dietary specialization has been overemphasized.

Specialized attributes of predators have traditionally been interpreted as adaptations for feeding on particular prey. In the case of *A. l. angelica*, the labral spine has usually been regarded as a specialization for feeding on barnacles. It may be, however, that this spine is also useful for penetrating bivalves at the valve margins, and that in still other cases, such as in predation on oysters, it has no obvious function. With the realization that diets are varied and generalized, structures such as the labral spine are perhaps best interpreted as adaptations that increase the size range of prey or decrease the time required for subduing victims.

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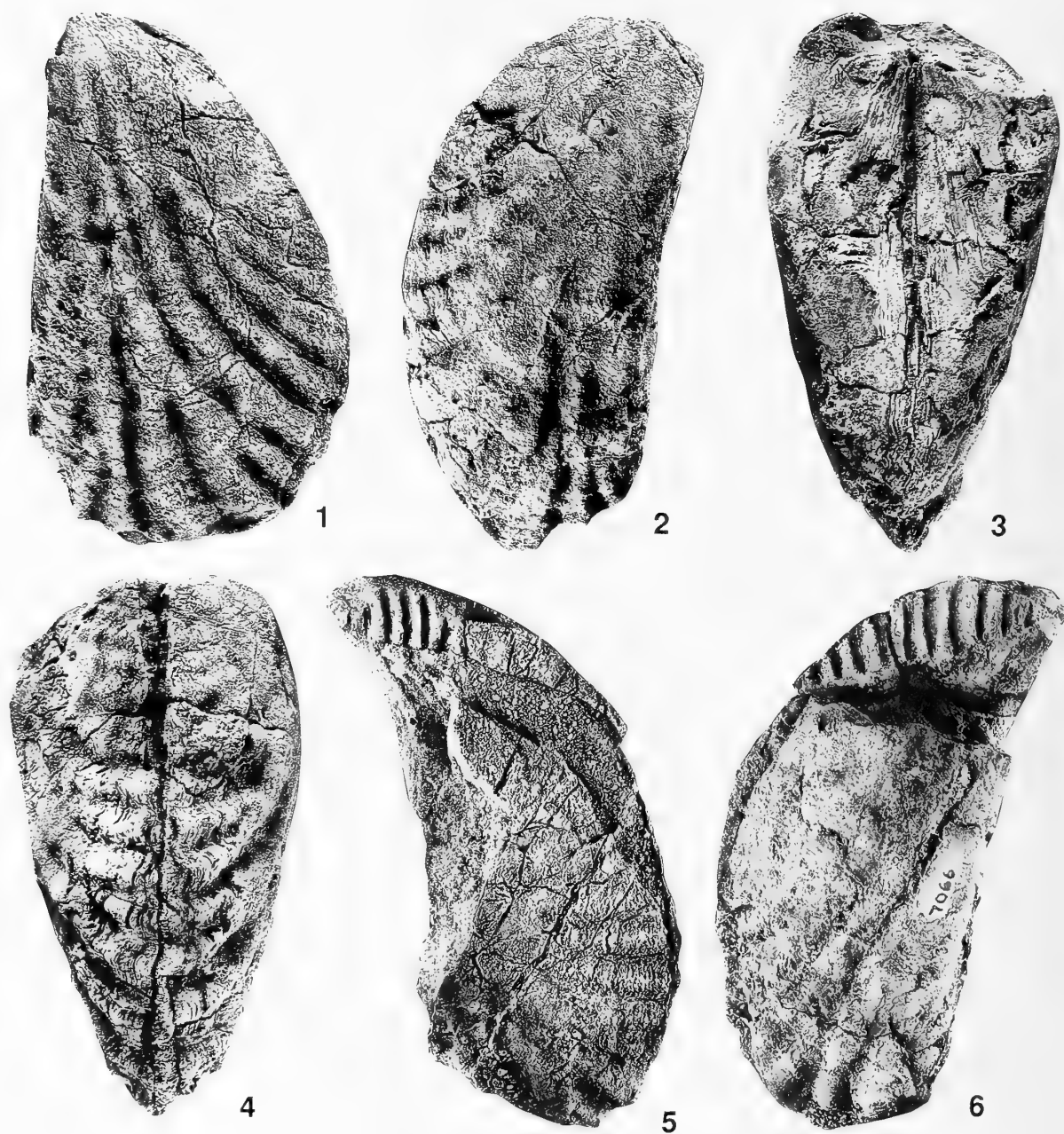
New Morphologic Information on the Bivalve *Isognomon (Isognomon) panzana* (Loel & Corey, 1932) from the Lower Miocene Vaqueros Formation, Southern California

by

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While searching through the University of California, Los Angeles invertebrate paleontology collections (now housed at the Natural History Museum of Los Angeles County, Invertebrate Paleontology Section = LACMIP), I recently came across several specimens of the early Miocene bivalve



Figures 1 to 6

Isognomon (Isognomon) panzana (Loel & Corey, 1932), Vaqueros Formation, LACMIP loc. 27066, Vaqueros Formation, Santa Ana Mountains, Orange County, southern California. Figure 1: hypotype LACMIP 12251, left-valve exterior, $\times 0.80$. Figures 2-4: hypotype LACMIP 12252, right-valve exterior, anterior, and posterior views, $\times 0.85$. Figure 5: hypotype LACMIP 12253, partial left-valve exterior with hingeline of right valve exposed, $\times 0.81$. Figure 6: hypotype LACMIP 12254, partial right-valve exterior with hingeline of left valve exposed, $\times 0.80$.

Isognomon (I.) panzana (Loel & Corey, 1932). Some of the specimens show much better preservation of the external sculpture than that of the worn holotypes and paratypes described and illustrated by Loel & Corey (1932: 187, pl. 9, figs. 1a, 1b, 2, 4, 5, 6). It is the purpose of this

note to provide better illustrations of the external sculpture of this species.

Moore (1983:84, pl. 25, figs. 3, 6) also illustrated the holotype and changed the taxonomic status of this species from *Pedalion panzana* Loel & Corey to *Isognomon (I.)*

panzana (Loel & Corey). The species is known only from the Vaqueros Formation of southern California and has been reported only with certainty from the type locality in the La Panza Mountains, eastern San Luis Obispo County, where specimens are locally abundant (Loel & Corey, 1932). The new specimens of the species are from the Vaqueros Formation at LACMIP loc. 27066 in the Santa Ana Mountains, and they represent the first confirmed report of this species from this area. Previously, only a tentatively identified single specimen of this species was reported from the west side of Plano Trabuco, southern Santa Ana Mountains (Loel & Corey, 1932:54). Schoellhamer et al. (1981), who reported the age of the Vaqueros Formation in this area to be early Miocene, also made macrofossil collections from the Vaqueros Formation but did not include *I. (I.) panzana* in their faunal lists.

The new specimens were collected by W. C. Corey, but he did not provide any detailed locality information. He identified the specimens as *Pedalion?* n. sp. There are nine specimens, ranging in length from 8 to 10.5 cm, and they are all closed-valved and complete or nearly complete.

Loel & Corey (1932:187) correctly reported that the surface of their species is "ornamented by a number of irregular, divaricate-radial plications, triangular in shape, which become more numerous and stronger toward the crenulate posterior ventral margin." The holotype (University of California Museum of Paleontology, Berkeley (= UCMP 31780) of *Isognomon (I.) panzana* is smooth due to poor preservation (Loel & Corey, 1932:pl. 9, fig. 1b). Two of the paratypes (UCMP 31783 and 31784) do possess indications of the external sculpture, but they are incomplete specimens (Loel & Corey, 1932:pl. 9, figs. 4, 6).

All of the new specimens show the irregular, divaricate-radial plications that become more numerous and stronger toward the valve margin, and the specimen that best shows these ribs is illustrated in Figure 1. Specimens illustrated in Figures 2, 5, and 6 also show these ribs but not as well because of poor preservation in the central regions of the valves. The new specimens also show the dorsal and ventral margins (Figures 3, 4), and these views are given because they have never been illustrated for *I. (I.) panzana*. Even though the radial ribs extend to the posterior ventral margin, the commissure of the valves is essentially smooth.

The radial ribbing of *I. (I.) panzana* resembles that seen in an ostreid now referred to by Moore (1987) as *Pycnodonte? (P.) howelli* (Wiedey, 1928) [= *Ostrea howelli* Wiedey]. The interiors of *I. (I.) panzana*, including the new specimens (Figures 5, 6), however, possess the hinge teeth characteristic of isognomid bivalves. The closed-valved specimens illustrated in Figures 5 and 6 are particularly important because they are the first specimens to photographically prove that the divaricate-radial ribs of *I. (I.) panzana* are associated with valves that possess the isognomid dentition. In order to expose the hingelines of these specimens, the parts of the opposing valve that formerly

covered the hingeline in each specimen had to be temporarily removed.

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Western Society of Malacologists Annual Meeting

The Twenty-seventh Annual Meeting of the Western Society of Malacologists will be held at the Miramar Hotel, located on the beach in Santa Barbara, California, from June 26 to 30, 1994. In addition to contributed papers on marine, freshwater, and terrestrial mollusks, both living and fossil, the agenda includes two special symposia, on "Molluscan biogeography—Past and present" (Co-chaired by Henry W. Chaney and Terrence M. Gosliner), and on "Micromollusks" (Chaired by James H. McLean). A shell auction, reprint sale, and banquet round out the program. The collections of the Santa Barbara Museum of Natural History will be open to all participants. For further information, please contact symposia chairmen, WSM President Kirstie L. Kaiser (% 475 N. Neil Armstrong Road, Salt Lake City, Utah 84116-2881), or WSM Treasurer Henry W. Chaney (Museum of Natural History, 2559 Puesta del Sol Road, Santa Barbara, California 93105; telephone, (805) 682-4711, ext. 334, or fax, 805-569-3170). Deadline for receipt of abstracts is May 15, 1994.

Fourth Edition of the International Code of Zoological Nomenclature

The International Commission on Zoological Nomenclature proposes to publish a new edition of the Code, taking into account the large number of possible amendments which have been received. It is planned that the Fourth Edition will be published during 1995 and that on January 1, 1996, its provisions will supersede those in the current (1985) edition.

The Commission's Editorial Committee met in Ham-

burg on October 12–16, 1993, to prepare a discussion draft for the new edition of the Code. Copies of this draft will be sent without charge to all subscribers to the *Bulletin of Zoological Nomenclature* and to members of the American and European Associations for Zoological Nomenclature. Any other institution or individual may order a copy from the Executive Secretary, I.C.Z.N., c/o The Natural History Museum, Cromwell Road, London SW7 5BD. Bank charges on currency exchange make it uneconomic to charge the cost of printing and postage (£3 or US\$5) except for payment in Sterling or US dollars. The draft will therefore be sent free of charge, but those able to pay in Sterling or US dollars are asked to enclose a check for £3 or US\$5 to cover the cost.

Before completing the definitive text of the Fourth Edition, the Commission will (in accordance with Article 16 of its Constitution) carefully consider all comments and suggestions on the draft. Zoologists and others are asked to send these to the Executive Secretary of the Commission at the above address as soon as convenient, and in any event not later than February 1995.

Conchologists of America Grant Program

The Conchologists of America, Inc., is pleased to announce that it is continuing its support of molluscan research by extending its grant program into 1994. Grants of up to \$1500 per application will be available to qualified persons

undertaking Recent or fossil, field or laboratory research. Applicants must outline the proposed project, the amounts and purposes for which the award will be used, including requested supplies, expendable equipment, living and/or travel expenses, or publication and illustration costs. The applicant should also submit a short biography that includes his or her educational status or pertinent job experience and a letter of recommendation from a scholastic or professional source.

The deadline for grant applications is May 1, 1994. They should be mailed in duplicate to

Dr. R. Tucker Abbott, Chairman
P.O. Box 1580
Sanibel, Florida 33957-1580 USA.

Applications are judged by the COA Grants Committee and awards will be made at the COA annual convention July 17–23, 1994, in Corpus Christi, Texas. Awards are made only to citizens or permanent residents of the Americas or to students attending graduate schools in the United States and do not cover salaries, overhead, permanent equipment, or conference or meeting costs.

If a grant is awarded, it is expected that the recipient will submit a brief, popular account of the project to the editor of *American Conchologist*. Grant recipients will be sent a sample article which may be used as a pattern for their reports.

BOOKS, PERIODICALS & PAMPHLETS

Sea Slugs of Western Australia

by FRED E. WELLS & CLAYTON W. BRYCE. 1993. Western Australian Museum, Perth. 184 pp.

This book documents much of the known opisthobranch fauna of Western Australia. In many respects, the fauna of western Australia resembles that of southern Africa, combining temperate endemic and widespread Indo-Pacific elements. The fauna is rich, and 226 species are beautifully illustrated in Clay Bryce's photographs. The layout, with no more than two species presented per page, maximizes the information contained in each photo.

The book has useful introductory material, beginning with a section describing what a sea slug is. Discussion and illustration of other organisms that are often confused with opisthobranchs, such as flatworms, onchidiid pulmonates, and lamellariid caenogastropods, will be useful to the novice. Opisthobranch collections are often full of these other organisms. Aspects of the feeding and developmental biology of opisthobranchs are presented in a clear and concise fashion. A brief biogeographical section discusses the composite nature of tropical and temperate faunas that blend together along the vast coastline of Western Australia. The bulk of the book deals with systematics. At the beginning of each family is an extremely useful synopsis of features that characterize the group, together with several recent systematic works that deal with that taxon.

Approximately 80 percent of the species presented in the book are widespread tropical species, while the remaining taxa are colder-water species, largely endemic to the temperate waters of Western Australia, South Australia, Victoria, New South Wales, and Tasmania.

Photographic documentation of even common species is important for several reasons. It is important to describe intraspecific variability within and between populations. These sorts of records also suggest areas for future systematic study. For example, *Aplysia* cf. *reticulata* appears similar to *A. juliana*. The specimen of *Bursatella leachi* is clearly distinct from the Indo-Pacific *Bursatella leachi leachi*, with far more elongate and branched processes. Clearly, systematic revision of *Bursatella* and its component "subspecies" is required. The species designated *Sclerodoris* sp. may be a species of *Aldisa*. Wells and Bryce illustrate two very different color forms of *Chromodoris bullocki*, suggesting that further study of these taxa is warranted. Also, the specimen identified as *Chromodoris* sp. cf. *africana* is dramatically different from western Indian Ocean specimens.

Included in the book are about 25 widespread Indo-Pacific species recorded here for the first time in Australian waters, and 28 unidentified and likely undescribed species. This marks a major contribution to our knowledge of the Indo-Pacific and Australian endemic faunas.

There are a few minor problems with presentation. For example, readers should be alerted to the fact that distributions are presented in clockwise fashion along the Australian coast (a fact that is buried in the introduction). This helps ascertain whether species known from both New South Wales and Western Australia have a northern or southern distribution. Some of the distributions presented are confusing. For example, *Tritonia* sp. is said to be found from Busselton to Quinns Rock; yet neither of these localities appears on the map on p. vii. This reduces the utility of the book to those not intimate with Western Australian geography. Some of the systematic placement of species can lead to confusion. Species of *Berthella*, *Berthellina*, and *Pleurobranchus* are interspersed, rather than all members of each genus being placed together. The same is true of species of Phyllidiidae, *Godiva*, and *Phyllodesmium*. *Phyllidiella zeylanica* is listed twice, as species 188 and 194.

The few problems cited above do not diminish appreciably the quality of this work or its scientific value to both sport diver and opisthobranch systematist. For anyone interested in opisthobranchs, this book is an essential addition to your library.

Terrence M. Gosliner

The Marine Flora and Fauna of Rottneest Island, Western Australia

edited by F. E. WELLS, D. I. WALKER, K. KIRKMAN, & R. LETHBRIDGE. 1993. Western Australian Museum, Perth. 2 vols., 634 pp.

In January 1991, under the auspices of the Western Australian branch of the Australian Marine Sciences Association, 36 marine biologists from Western Australia, the eastern states of Australia, and other countries met at Rottneest Island on the west coast of Western Australia to conduct research for 18 days on the marine flora and fauna of the island. These two volumes, the Proceedings of that workshop, contain 34 original papers on the taxonomy, ecology, behavior, morphology, and physiology of local species. The opening paper is an overview of the marine environment of Rottneest Island by F. E. Wells and D. I. Walker. Fourteen of the papers focus specifically on mollusks. Others involve the taxonomy of marine plants, maritime mites, crustaceans, echinoderms, and annelids. Several of these represent catalogues of the members of their groups from Rottneest Island; nothing of equivalent scope was attempted for the mollusks as a whole.

Molluscan taxonomic papers include ones on *Parastrphia* (Gastropoda: Caecidae) by H. P. I. Hughes; vermetid

gastropods by R. N. Hughes; Sacoglossa from Rottnest Island and central Western Australian by K. R. Jensen; a new commensal bivalve (Montacutidae) by P. G. Oliver; and a new cerithiid gastropod by W. F. Ponder.

Ecological and behavioral contributions include: "Observations on *Antisabia foliacea* (Quoy and Gaimard, 1835) (Mollusca, Gastropoda, Prosobranchia, Hipponicidae) from off Rottnest Island, Western Australia," by J. Kundsén; "Episodic mortality of limpets on a shore platform at Rottnest Island, Western Australia" and "Development and early life history of three temperate Australian species of *Conus* (Mollusca: Gastropoda)," by A. J. Kohn; "The ecology, diet and foraging strategy of *Thais orbita* (Gastropoda: Muricidae) on a rocky shore of Rottnest Island, Western Australia," by B. Morton and J. C. Britton; "Comparative ecology of a biogeographically heterogeneous *Conus* assemblage," by A. J. Kohn and K. N. Almasi; "The ecology of the giant limpet *Patella laticostata* on intertidal limestone platforms at Rottnest Island, Western Australia," by R. E. Scheibling and R. Black; and "Dietary and anatomical specialization of mitrid gastropods (Mitridae) at Rottnest Island, Western Australia," by J. D. Taylor. Physiology and functional morphology are represented by "The effects of experimental protocol and behavior on evaporative water loss during emersion in three species of rocky shore gastropods," by J. C. Britton; and "An analysis of heat and desiccation stresses as critical environmental factors on a rocky shore," by M. W. Yipp (dealing with prosobranch and pulmonate limpets).

The books are well produced paperbacks, with good quality line and photographic illustrations, and are available from the Western Australian Museum, Francis Street, Perth, 6000 Australia.

B. Roth

**The Banana Slug.
A Close Look at a Giant Forest Slug of
Western North America**

by ALICE BRYANT HARPER, with photographs by DANIEL HARPER. Third printing, revised. 1993. Bay Leaves Press,

160 Robideaux Road, Aptos, California 95003 (in cooperation with the Santa Cruz Museum Association). 32 pp. Price: \$7.95.

Now in its third printing and continuing to sell well in a number of west coast parks and bookshops from California to British Columbia, *The Banana Slug* by now may be one of the most widely read books on North American mollusks in print. The third printing differs from previous printings in presenting an improved distribution map and reference to the recently confirmed occurrence of *Ariolimax* on Palomar Mountain, southern California.

We continue to recommend this small book for its effective presentation of solid information at a popular level. It is noteworthy for containing the only published live-action photographs of the peculiar process of apophallation, wherein after copulation the male intromittent organ is not withdrawn from the partner but is gnawed off near its base. The author correctly notes that the longstanding "explanation" of this behavior—that the large size of the copulatory organs causes them to become stuck during mating—is only one of several interpretations. Hypotheses involving sexual conflict in a hermaphroditic mating system seem especially worth investigating. Leonard's (1991, *American Malacological Bulletin* 9(1):53–54) brief review of *Ariolimax* mating behavior, with suggestions for further study, is a good place for the enterprising experimenter to start. The role of the structure that Mead (1943, *American Midland Naturalist* 30(3):679) named the *intrinsic muscle* of the vagina (does it clamp the partner's inserted male organ to prevent release of sperm, while the individual delivers its own sperm to the mate?) also deserves investigation in this context.

B. Roth

The Editor regrets that the name of Janet R. Voight was misspelled at the end of her book review in *The Veliger* 36(4):434.

Manuscripts

Manuscripts must be typed, one side only, on A4 or equivalent (e.g., 8½" × 11") white paper, and double-spaced throughout, including references, figure legends, footnotes, and tables. All margins should be at least 25 mm wide. Text should be ragged right (i.e., not full justified). Avoid hyphenating words at the right margin. Manuscripts, including figures, should be submitted in triplicate. The first mention in the text of the scientific name of a species should be accompanied by the taxonomic authority, including the year, if possible. Underline scientific names and other words to be printed in italics; no other manipulation of type faces is necessary on the manuscript. Metric and Celsius units are to be used. For aspects of style not addressed here, please see a recent issue of the journal.

The Veliger publishes in English only. Authors whose first language is not English should seek the assistance of a colleague who is fluent in English before submitting a manuscript.

In most cases, the parts of a manuscript should be as follows: title page, abstract, introduction, materials and methods, results, discussion, acknowledgments, literature cited, figure legends, footnotes, tables, and figures. The title page should be a separate sheet and should include the title, authors' names, and addresses. The abstract should be less than 200 words long and should describe concisely the scope, main results, and conclusions of the paper. It should not include references.

Literature cited

References in the text should be given by the name of the author(s) followed by the date of publication: for one author (Phillips, 1981), for two authors (Phillips & Smith, 1982), and for more than two (Phillips et al., 1983). The reference need not be cited when author and date are given only as authority for a taxonomic name.

The "literature cited" section should include all (and only) references cited in the text, listed in alphabetical order by author. Each citation must be complete, with all journal titles *unabbreviated*, and in the following forms:

a) Periodicals:

Hickman, C. S. 1992. Reproduction and development of trochacean gastropods. *The Veliger* 35:245-272.

b) Books:

Bequaert, J. C. & W. B. Miller. 1973. *The Mollusks of the Arid Southwest*. University of Arizona Press: Tucson. xvi + 271 pp.

c) Composite works:

Feder, H. M. 1980. Asteroidea: the sea stars. Pp. 117-135 in R. H. Morris, D. P. Abbott & E. C. Haderlie (eds.), *Intertidal Invertebrates of California*. Stanford University Press: Stanford, Calif.

Tables

Tables must be numbered and each typed on a separate sheet. Each table should be headed by a brief legend. Avoid vertical rules.

Figures and plates

Figures must be carefully prepared and submitted ready for publication. Each should have a short legend, listed on a sheet following the literature cited. Text figures should be in black ink and completely lettered. Keep in mind page format and column size when designing figures. Photo-

graphs for halftone reproduction must be of good quality, trimmed squarely, grouped as appropriate, and mounted on suitably heavy board. Where appropriate, a scale bar may be used in the photograph; otherwise, the specimen size should be given in the figure legend. Photographs should be submitted in the desired final size.

Clear xerographic copies of figures are suitable for reviewers' copies of submitted manuscripts. It is the author's responsibility to ensure that lettering will be legible after any necessary reduction and that lettering size is appropriate to the figure.

Use one consecutive set of Arabic numbers for all illustrations (that is, do not separate "plates" from "text figures").

Processing of manuscripts

Each manuscript is critically evaluated by at least two reviewers. Based on these evaluations the editor makes a preliminary decision of acceptance or rejection. The editor's decision and the reviewers' comments are sent to the author for consideration and further action. Unless requested, only one copy of the final, revised manuscript needs to be returned to the editor. The author is informed of the final decision and acceptable manuscripts are forwarded to the printer. The author will receive proofs from the printer. One set of corrected proofs should be mailed promptly to the editor after review. Changes other than the correction of printing errors will be charged to the author at cost.

An order form for the purchase of reprints will accompany proofs. Reprints are ordered directly from the printer.

Authors' contributions

The high costs of publication require that we ask authors for a contribution to defray a portion of the cost of publishing their papers. However, we wish to avoid a handicap to younger contributors and others of limited means and without institutional support. Therefore, we have adopted the policy of asking for the following: \$30 per printed page for authors with grant or other institutional support and \$10 per page for authors who must pay from their personal funds (2.5 double-spaced manuscript pages normally equal one printed page). This request is made only after the publication of a paper; these contributions are unrelated to the acceptance or rejection of a manuscript, which is entirely on the basis of merit. In addition to this requested contribution, authors of papers with an unusually large number of tables or figures will be asked for an additional contribution. Because these contributions by individual authors are voluntary, they may be considered by authors as tax-deductible donations to the California Malacozoological Society, Inc.

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NOTES, INFORMATION & NEWS

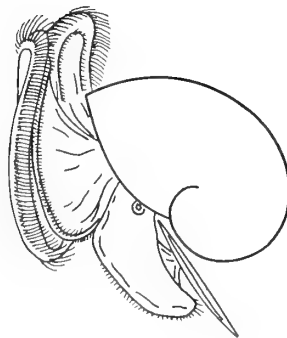
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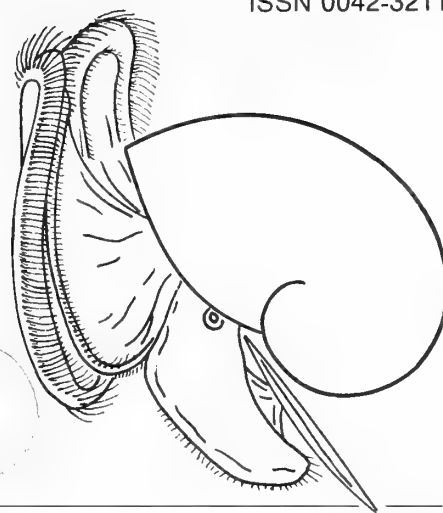
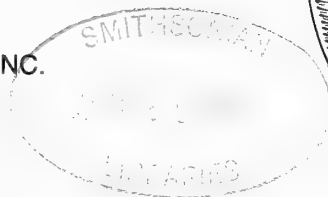


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ISSN 0042-3211

THE VELIGER

A Quarterly published by
CALIFORNIA MALACOOLOGICAL SOCIETY, INC.
Berkeley, California
R. Stohler, Founding Editor



Volume 37 July 1, 1994 Number 3

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The Veliger (ISSN 0042-3211) is published quarterly on the first day of January, April, July, and October. Rates for Volume 37 are \$32.00 for affiliate members (including domestic mailing charges) and \$60.00 for libraries and nonmembers (including domestic mailing charges). For subscriptions sent to Canada and Mexico, add US \$4.00; for subscriptions sent to addresses outside of North America, add US \$8.00, which includes air-expedited delivery. Further membership and subscription information appears on the inside cover. The Veliger is published by the California Malacozoological Society, Inc., % Santa Barbara Museum of Natural History, 2559 Puesta del Sol Road, Santa Barbara, CA 93105. Second Class postage paid at Berkeley, CA and additional mailing offices. POSTMASTER: Send address changes to The Veliger, Santa Barbara Museum of Natural History, 2559 Puesta del Sol Road, Santa Barbara, CA 93105.

THE VELIGER

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Two New Genera of Hydrobiid Snails (Prosobranchia: Rissooidea) from the Northwestern United States

by

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Abstract. Based on morphological study of recently collected material, *Bythinella hemphilli*, distributed within the lower Snake-Columbia River basin, is transferred to a new genus, *Pristinicola*; and *Taylorconcha serpenticola*, new genus and new species, a federally listed taxon restricted to a short reach of the Middle Snake River in Idaho and previously known by the common name, Bliss Rapids Snail, is described. These genera do not appear closely related either to one another or to other North American Hydrobiidae.

INTRODUCTION

Among the large freshwater molluscan fauna of the United States, prosobranch snails of the family Hydrobiidae compose one of the most diverse groups, totaling about 170 described species. Although the state of knowledge of these minute animals has greatly increased in the past 25 years through the combined efforts of several researchers, much work remains to be done, including assessment of the taxonomic status and relationships of poorly known nomina and treatment of a large undescribed fauna.

In the northwestern United States, generic diversity of hydrobiids is low, and relatively few described species are

known. Perhaps the most significant unresolved question pertaining to the local described fauna involves the status of *Bythinella hemphilli*. Pilsbry's original placement of this species in *Bythinella*, which is otherwise known only from Europe (Bănărescu, 1990:342), has long been questioned, and two other generic assignments have been offered. Most recent compilations treat this snail as *incertae sedis* (i.e., Burch & Tottenham, 1980:130; Burch, 1989:130). An undescribed fauna of uncertain diversity also occurs in this region and includes a federally listed species from the Snake River of Idaho, commonly known as the Bliss Rapids Snail, which has been treated in the literature as an undescribed genus, based on the unpublished studies of

Taylor (1982). Recent fieldwork in this region has permitted large collections of these two snails, and laboratory studies have suggested that these represent new genera, which we describe below.

MATERIALS AND METHODS

Institutional repositories of examined specimens are indicated by the following abbreviations: ANSP, Academy of Natural Sciences, Philadelphia; UF, Florida Museum of Natural History, Gainesville; and USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Anatomical study was of alcohol-preserved snails that had been relaxed with menthol crystals and fixed in dilute (about 4%) formalin. Inorganic shell material was removed by soaking specimens in Bouins solution or hydrochloric acid. Animals were dissected in dilute Bouins solution. Specimens were first examined entire, after which the visceral coil was separated from the proximal portion of the animal by tearing between the anterior edge of the style sac and the kidney/pericardium. The pallial roof then was torn from the head-foot, flattened out, and pinned. The female glandular oviduct and associated structures were examined from the left side. The RPG ratio is defined as length of the pleuro-supraesophageal connective divided by the sum of lengths of supraesophageal ganglion, pleuro-supraesophageal connective, and right pleural ganglion (Davis et al., 1976:263). Anatomical illustrations were prepared from camera lucida drawings.

Shell, opercula, and radula were cleansed in commercial bleach (CLOROX), rinsed in water, and then studied and photographed using a Hitachi S-570 Scanning Electron Microscope (SEM). Animals were dried using a Denton DCP-1 Critical Point Drier and studied with SEM to ascertain ciliation patterns on dorsal surfaces of tentacles and penis. Whole mounts of penes were prepared by staining in hematoxylin followed by dehydration, clearing, and mounting in balsam. Serial sections were cut at 4 μ m and stained with hematoxylin and eosin. Morphological characters were selected, in part, from those listed by Ponder et al. (1993).

SYSTEMATIC TREATMENT

Superfamily RISSOOIDEA Gray, 1847

Family HYDROBIIDAE Troschel, 1857

Subfamily LITHOGLYPHINAE Troschel, 1857

Pristinicola Hershler, Frest, Johannes,
Bowler & Thompson, gen. nov.

Type species: *Bythinella hemphilli* Pilsbry, 1890: monotypy.

Etymology: Latin *pristinus*, pristine, and *cola*, dweller (Masculine [per ICZN Article 30[a][i]]); referring to occurrence of this snail in undisturbed habitats.

Diagnosis: Shell small to medium-sized, narrowly-conic, smooth, whorls near flat to moderately convex, with umbilicus absent or weakly rimate. Aperture simple; inner lip complete; peristome thickened within. Protoconch about 1.5 whorls, finely wrinkled. Operculum thickened, horny, red-brown, paucispiral, with attachment scar margin thickened along inner edge and large attachment scar callus. Radula with central teeth having a single pair of basal cusps; cusp formula of central teeth, (4-5)-1-(4-5); lateral teeth, 3-1-(4-5). Stomach without posterior appendix and with single opening to digestive gland. Cephalic tentacles with fairly heavy, uniform ciliation. Animal pale except for black eyespots. Penis narrow-elongate, without accessory lobes or glands. Female capsule gland with enclosed ventral channel and three distinct glandular zones.

Remarks: Despite the "*Bythinella*-like" shape of their shells, these animals clearly do not belong either to this genus or, more generally, to the subfamily Emmericiinae, as that group is diagnosed, in part, by a penis having accessory glands and lobes, and absence of a female seminal receptacle (Radoman, 1983; Hershler et al., 1990).

Pristinicola and the genus described below share with numerous other freshwater genera a penis lacking lobes or large glands, female capsule gland with the ventral channel completely enclosed, and direct development. The relationships of the various members of this group, both to one another and to other hydrobiids, are poorly understood, although it is likely that these snails were derived from primitive brackish-water or estuarine members of the family (Ponder, 1988b). Of these taxa, several genera of fluviatile snails with large, globose shells from North America, South America, and Europe compose a compact group that has been accorded subfamily status (Lithoglyphinae) by some workers. However, none of the diagnostic character states of the subfamily listed by Thompson (1984) can be considered unequivocal synapomorphies, and the group could represent a polyphyletic assemblage of convergent forms, or a paraphyletic subset of a clade having broader habitat and shell form diversity. (The latter was recently suggested by Hershler & Thompson [1990], who broadened the concept of the "subfamily" by inclusion of several North American genera of subterranean snails.)

Of the eight diagnostic features of the Lithoglyphinae listed by Thompson (1984:123), each of our two new genera only possesses three such features: both lack a posterior appendix of the stomach and have a simple penis; *Pristinicola* has basal cusps originating from the face of the central radular tooth; and the genus described below has spiral sculpture on the protoconch. All four of the above features are in fact widely distributed among other genera of the family. Note also that the penis of our snails does not closely conform to that of lithoglyphines, which approximates a broad, flat blade and is perhaps the key character state defining this group. In light of the above, it may be premature to assign our two new genera to a particular hydrobiid subfamily. We expect that a com-

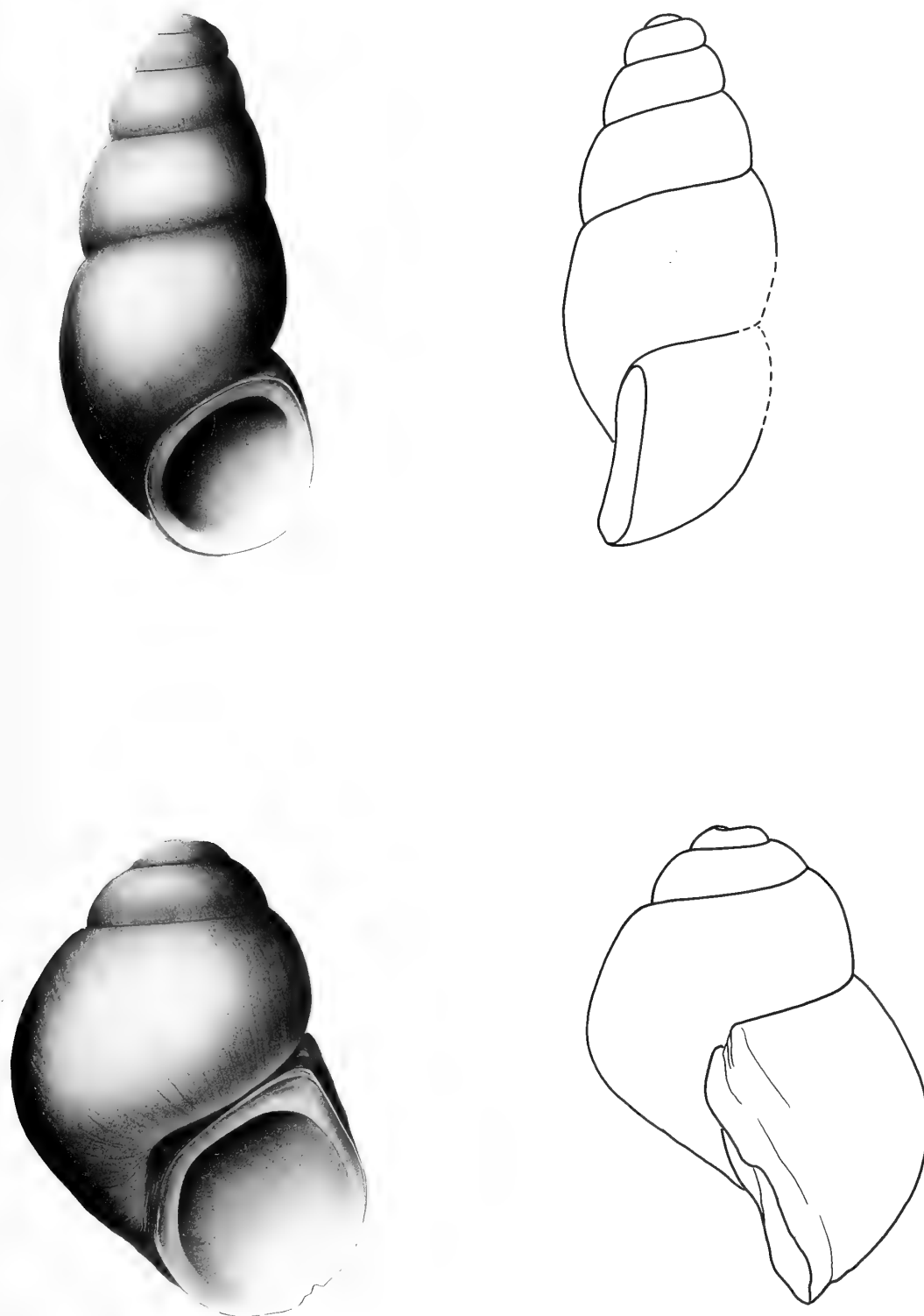
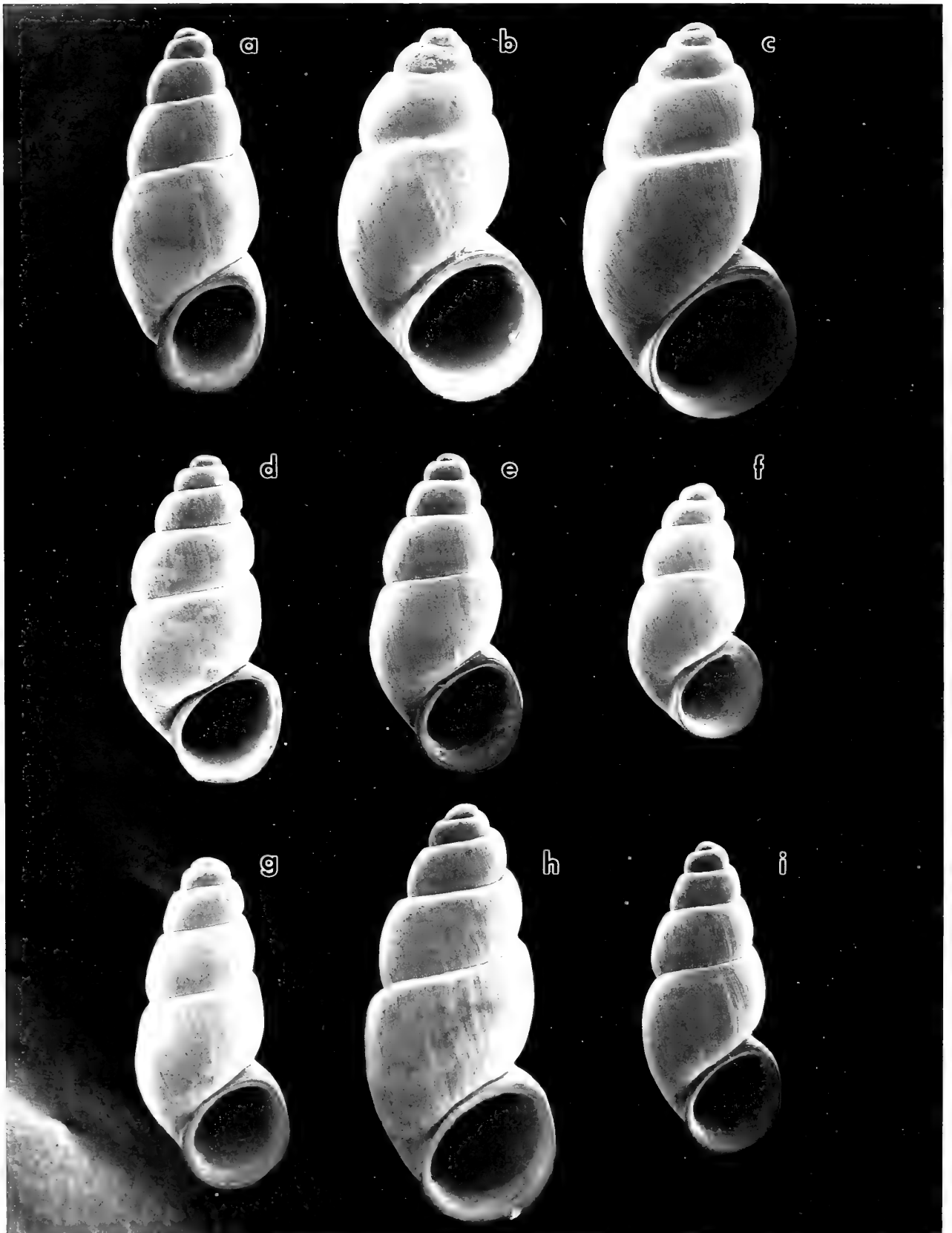


Figure 1

Lectotype, *Pristinicola hemphilli*, ANSP 31176, shell height, 2.7 mm (top row); holotype, *Taylorconcha serpenticola* Hershler, Frest, Johannes, Bowler & Thompson, gen. et sp. nov., USNM 860583, shell height, 2.45 mm (bottom row).



prehensive anatomical survey of "lithoglyphine" taxa will lead to a better resolution of these problems.

Neither of our two new genera is closely similar to any other genus of North American Hydrobiidae. *Pristinicola* differs from the genus described below by numerous characters, including its narrower shell, wrinkled protoconch microsculpture, uniform pattern of tentacle ciliation, elongate salivary glands, relatively shorter radula, larger basal cusps on the central radula teeth, strongly developed anterior pedal mucous gland, fingerlike ctenidial filaments, strongly undulating penial duct, three distinct capsule gland zones, and presence of a bursa copulatrix.

***Pristinicola hemphilli* (Pilsbry, 1890)**

(Figures 1 [top row], 2–7)

Bythinella hemphilli Pilsbry, 1890:63 (Lectotype [fide Baker, 1964:173; Richardson et al., 1991:67], ANSP 31176) (Figure 1 [top row]). Hannibal, 1912:186 (as synonym of *Paludestrina protea*). Clench & Turner, 1962:64. Baker, 1964:173. Anderson & Pratt, 1965:13. Anderson et al., 1966:704. Turgeon et al., 1988:60. Richardson et al., 1991:67.

P[aludestrina]. hemphilli. Pilsbry, 1899:122.

Paludestrina hemphilli. Walker, 1918:137. Henderson, 1924:191. Henderson, 1929:166.

Hydrobia hemphilli. Henderson, 1936a:138. 1936b:277.

"*Bythynella*" *hemphilli*. Taylor, 1975:94.

"*Bythynella*" *hemphilli*. Burch & Tottenham, 1980:130 (fig. 320). Burch, 1989:130 (fig. 320).

Description: Shell (Figures 1 [top row], 2) narrowly-conic, almost pupiform; clear-white; length, 1.7–3.1 mm; total whorls 4.25–5.50. Apex blunt; protoconch about 1.5 whorls, finely wrinkled (Figure 4a), often eroded. Teleoconch whorls near flat to moderately convex, with shallow sutures; rarely with adapical shoulder or subsutural angulation. Teleoconch sculpture of weak collabral growth lines, often accompanied by numerous faint spiral striae. Aperture ovate-elongate, rounded or expanded below, rounded or slightly angled above. Inner lip complete, fairly thick, especially adapically, slightly reflected, adnate or very slightly separated from body whorl. Outer lip slightly thickened, straight or slightly curved, usually opisthoclinal, sometimes orthoclinal. Umbilicus (usually) absent or weakly rimate. Periostracum tan-light brown, often covered by dark, thick deposits. Shell measurements are in Table 1.

Operculum (Figure 3) horny, fairly thick, ovate, red-brown; nucleus eccentric; dorsal surface unfrilled. Attachment scar margin usually strongly thickened along inner edge, with weaker scar along outer edge. Attachment scar callus fairly large, raised.

Table 1

Shell measurements of *Pristinicola hemphilli*. WH, number of whorls; SL, shell length; SW, shell width; LBW, length of body whorl; AL, aperture length; AW, aperture width.

	WH	SL	SW	LBW	AL	AW
Lectotype	5.0	2.73	1.29	1.68	0.89	0.89
Paralectotype	5.0	2.57	1.29	1.62	0.85	0.84
Paralectotype	5.0	2.48	1.17	1.54	0.81	0.84
USNM 874627, <i>n</i> = 9						
Mean	5.0	2.42	1.21	1.52	0.85	0.86
SD	0.004	0.12	0.08	0.06	0.06	0.03
USNM 874424, <i>n</i> = 9						
Mean	4.9	2.32	1.12	1.43	0.77	0.80
SD	0.2	0.17	0.07	0.11	0.05	0.06
USNM 874184, <i>n</i> = 9						
Mean	4.5	2.84	1.55	2.01	1.11	1.13
SD	0.1	0.15	0.07	0.10	0.05	0.05
USNM 874626, <i>n</i> = 5						
Mean	5.0	2.46	1.16	1.47	0.85	0.84
SD	0.2	0.19	0.07	0.09	0.06	0.06
USNM 758255, <i>n</i> = 9						
Mean	4.9	2.73	1.37	1.73	0.95	1.02
SD	0.2	0.25	0.09	0.13	0.08	0.09

Tentacle ciliation fairly heavy, of generally uniform nature (Figure 4b–d). Distal tip of tentacle without elongate setae. Snout slightly longer than tentacles, about as long as wide, with well-developed distal lobes (in preserved material). Eyelobes absent. Foot ovate-elongate; anterior end slightly convex, with well-developed lateral wings; posterior end rounded. Anterior mucous gland of separate glands; central gland about as long as adjacent units. Animal pale except for black eyes.

Buccal mass small relative to snout; jaws present. Salivary glands elongate. Dorsal folds of esophagus simple.

Radular ribbon about 0.85 × 0.08 mm, with approximately 85 rows of teeth; ribbon with medium-sized coil behind buccal mass. Central radular tooth (Figure 5a, b) broadly trapezoidal, with strongly indented dorsal edge. Lateral angles short. Basal process narrow; basal sockets deep. Central cusp pointed, up to twice as long as lateral cusps; lateral cusps, four to five. Basal cusp single, large, arising from outer portion of tooth face. Lateral tooth (Figure 5c–e) with central cusp flanked by three inner cusps and four to five outer cusps; cusps pointed. Basal

Figure 2

Scanning electron micrographs of shells of *Pristinicola hemphilli*. a. paralectotype, ANSP 368405, shell height, 2.7 mm. b, c. USNM 874184. d. UF 45976. e. USNM 874424. f, i. USNM 874440. g, h. USNM 874429. All photographs are printed to the same scale.



cusps of lateral tooth well developed; lateral wing about twice as long as cutting edge. Marginal teeth (Figure 5c-f) with small cusps (inner tooth, 16-22; outer, about 23) and weakly developed wings on inner sides.

Stomach chambers poorly differentiated, but appearing about equal in length; posterior appendix absent. Stomach proper about one and one-half times as long as style sac, with single opening to digestive gland. Rectum without arch in pallial cavity; fecal pellets usually oriented longitudinally. Anus positioned near mantle edge, slightly anterior to anterior end of capsule gland.

Mantle edge simple. Organs and structures of pallial cavity shown in Figure 6a. Ctenidium extending to pericardium to slightly posterior to mantle edge; efferent vein short. Filaments about 16, short, finger-shaped, with near central apex. Osphradium broadly ovate with thickened margin, about 20% of ctenidium length, centered slightly posterior to middle of ctenidial axis. Hypobranchial gland poorly developed, near smooth. Kidney with about third of length in pallial roof. Renal gland weakly developed, longitudinal. Renal aperture small, weakly differentiated. Body spaces with very little connective tissue.

Testis, one whorl, composed of broad, vertical, dorsally branched lobes connected ventrally by narrow vas efferens. Testis filling about half of length of visceral coil behind stomach and extending over posterior stomach chamber. Vas deferens exiting from ventral testis near anterior edge. Seminal vesicle small coiled mass underneath anteriormost testis. Prostate gland of complex histology, elongate, bean-like, with third to slightly less than half of length in pallial roof. Prostate gland elongate oval in section; wall of medium thickness all around; lumen narrow, simple. Pallial vas deferens exiting slightly behind anterior end of prostate gland. Pallial vas deferens loosely embedded in connective tissue on pallial roof; posterior section without coil, but curving onto columellar muscle; anterior section straight, on pallial floor in connective tissue.

Penis (Figures 4e, f, 6b) originating well behind left tentacle; narrow-elongate, slightly tapered distally, without lobes; small relative to head, extending only slightly anterior to mantle edge. Basal portion expanded, with few deep folds; penis otherwise simple or with scattered folds. Distal tip of penis (Figure 4f) tapering, with small terminal papilla. Penial duct strongly undulating; opening terminal, simple. Distal penis with scattered bunches of cilia.

Ovary simple sac filled with about 10 oocytes, 1.0 whorl, filling slightly less than half of the visceral coil behind the stomach, and very slightly overlapping the posterior stom-

ach chamber. Distal female genitalia shown in Figure 6c, d. Glandular oviduct of complex histology. Capsule gland simple, as long or slightly longer than albumen gland, composed of very short, clear, posterior section; amber, deeply creased middle section; and long, amber-clear, anterior section. Lateral walls of capsule gland thick; ventral wall thin. Genital aperture small, subterminal pore without anterior vestibule. Albumen gland simple, white, with about 25% of length in pallial roof. Coiled oviduct large, fairly thick, smooth, bound in connective tissue; composed of initial anterior bend followed by tight, circular twist. Bursa copulatrix large, non-muscular, strongly reflexed, with short proximal portion and distal portion extending from just posterior to albumen gland forward over much of dorsal albumen gland. Lumen of bursa copulatrix containing fluid and digested sperm. Bursal duct positioned near ventral edge of albumen gland, fairly short, slightly narrower than proximal bursa copulatrix, opening to oviduct slightly anterior to coiled portion. Seminal receptacle about half as long as bursa copulatrix, broadly ovate, with fairly thickened muscular coat; positioned along ventral edge but largely posterior to albumen gland, overlapped dorsally by bursa copulatrix, oblique or transverse relative to long axis of albumen gland. Lumen of seminal receptacle containing oriented sperm. Seminal receptacle duct about third as long and slightly narrower than sac, opening to oviduct just posterior to opening of bursal duct.

RPG ratio 36%. Cerebral and pedal commissures elongate.

Type locality: Near Kentucky Ferry, Snake River, Washington. This site has never been precisely located (see Henderson, 1936a), but may have been in reference to the Kentuck Trail, which extended from the Snake River in Washington northeast to the Spokane Bridge along the Idaho border (see Freeman, 1954). (Alternatively, Hemphill could have been referring to Central Ferry, an old town on the Snake River in Whitman County, Washington, which was the site of one of the earliest established ferries on the Washington Snake River, and along the old route to Lewiston and Spokane.) There were at least five ferry crossings along a 24 km reach of the Snake River near the origin of the Kentuck Trail: Lyons, Texas, Kentucky, Penawawa, and Central ferries. The Kentuck Ferry was also called the Ruark-Davidson Ferry, Blackfoot Ferry, and Angell Ferry. The exact location of this ferry is difficult to ascertain, as crossing places depended in part on season and local river conditions. Furthermore, there

Figure 3

Scanning electron micrographs of opercula of *Pristinicola hemphilli*, USNM 874184. a. Dorsal operculum, bar = 250 μ m. b-d. Ventral opercula, bar = 231 μ m.

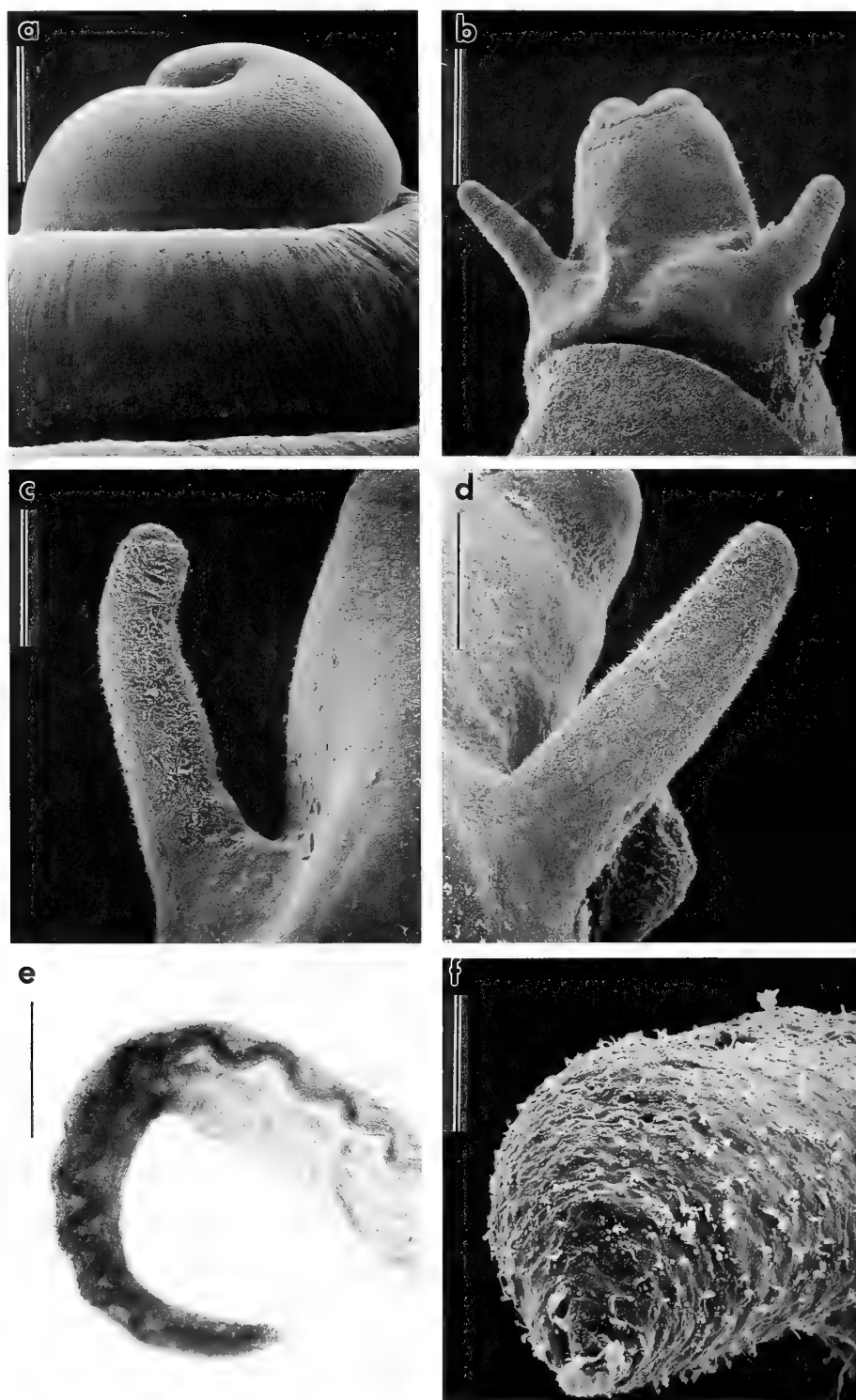


Figure 4

Photographs and scanning electron micrographs of protoconch, head, and penis of *Pristinicola hemphilli*, USNM 874184. a. Protoconch, bar = 120 μm . b. Critical point dried head, bar = 0.43 mm. c. Dorsal surface of critical point dried left tentacle, bar = 176 μm . d. Dorsal surface of right tentacle, scale as in c. e. Whole mount of penis, bar = 0.25 mm. f. Distal tip of critical point dried penis, bar = 38 μm .

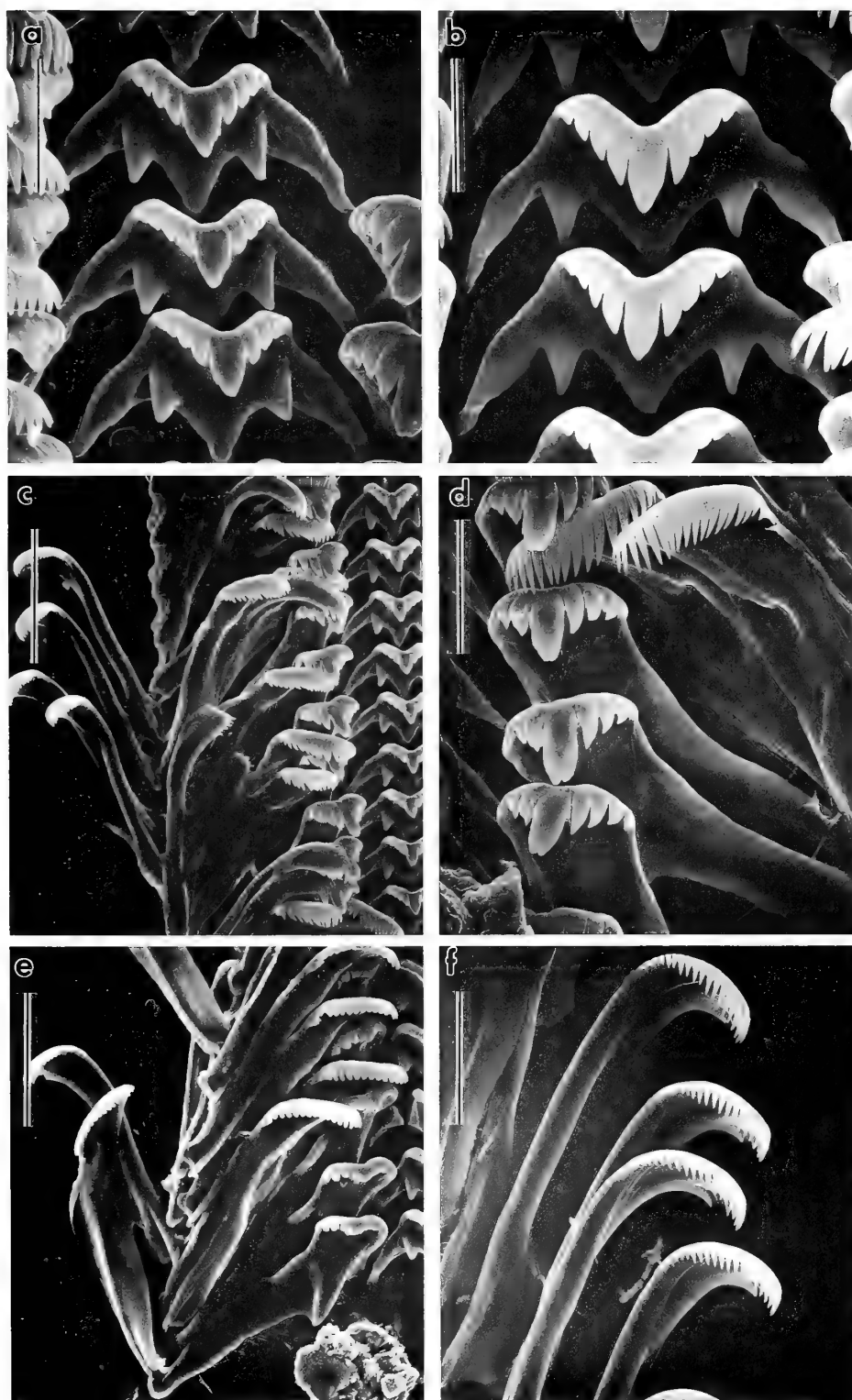


Figure 5

Scanning electron micrographs of radula of *Pristinicola hemphilli*. a. Central radular teeth, USNM 874184, bar = 10 μm. b. Central radular teeth, UF 45971, bar = 5 μm. c-e. Lateral and marginal teeth, USNM 874184, bars = 27 μm, 12 μm, 23.1 μm. f. Outer marginal teeth, USNM 874184, bar = 12 μm.

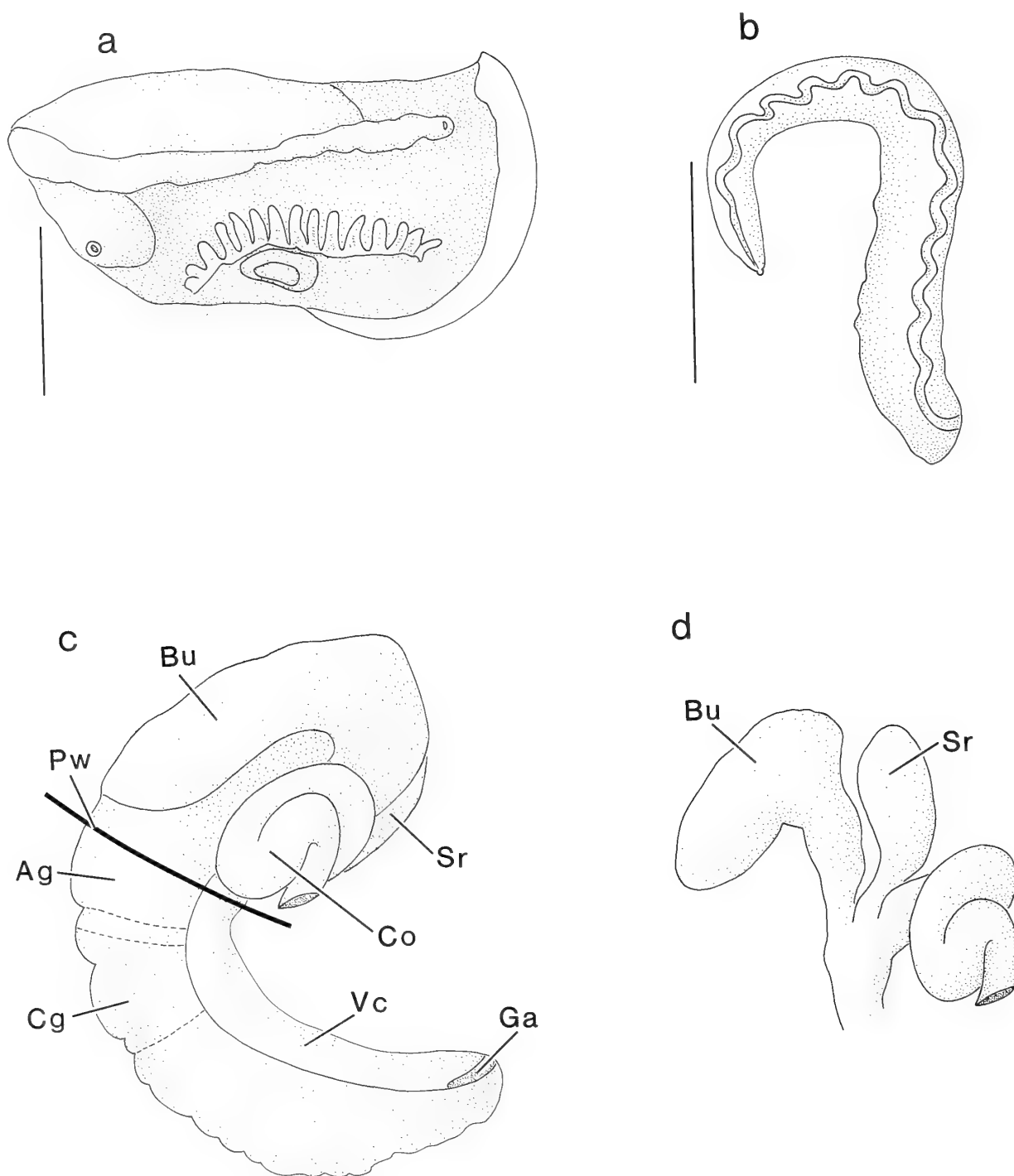


Figure 6

Anatomy of *Pristinicola hemphilli*, USNM 874184. a. Contents of pallial cavity, bar = 0.25 mm. b. Penis, bar = 0.5 mm. c. Distal female genitalia, left side, scale as in b. d. As in c, but with albumen gland removed and coiled oviduct shifted to completely expose seminal receptacle and bursa copulatrix. Ag, albumen gland; Bu, bursa copulatrix; Cg, capsule gland; Co, coiled oviduct; Ga, genital aperture; Pw, pallial wall; Sr, seminal receptacle; Vc, ventral channel.

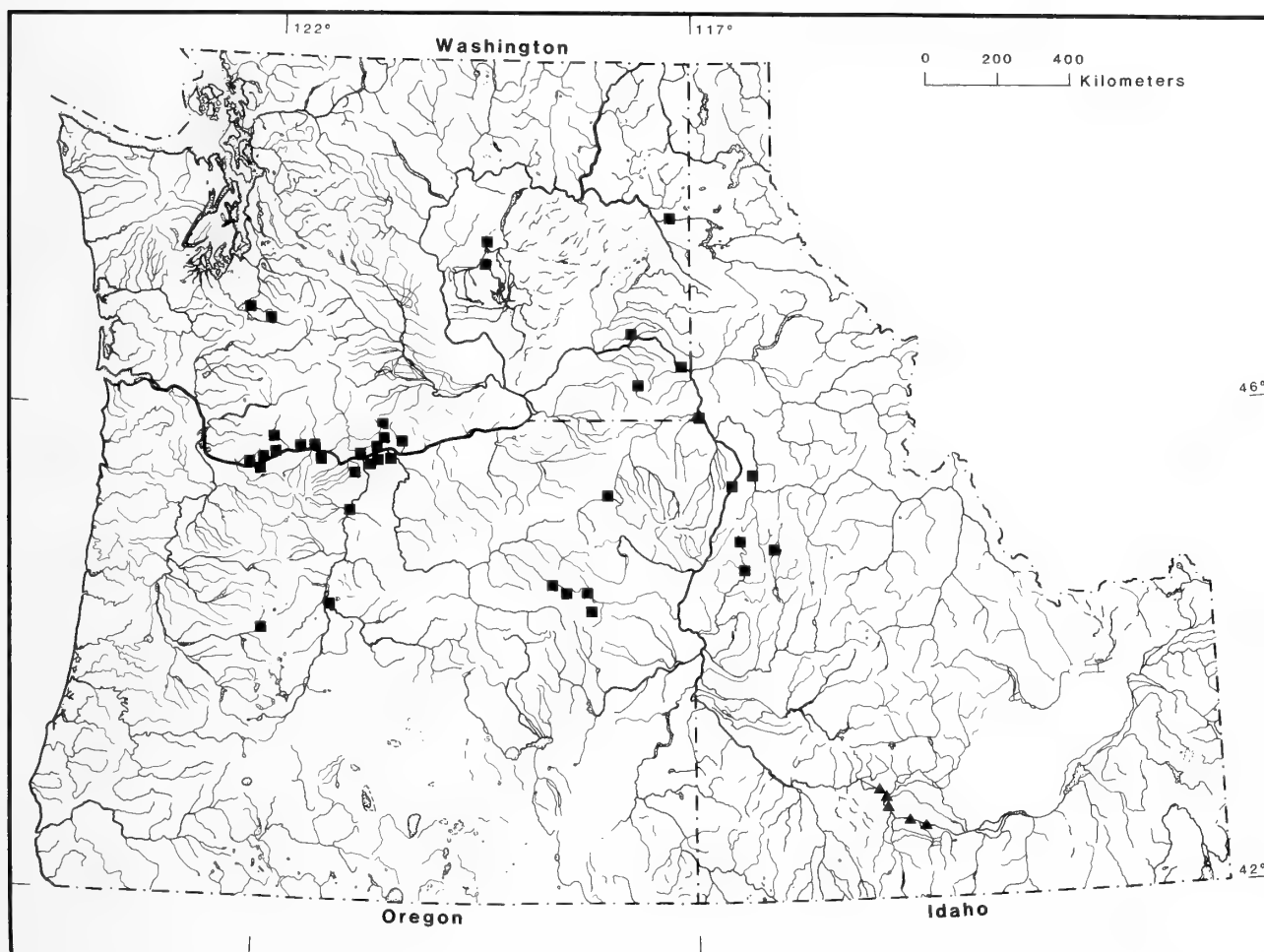


Figure 7

Distribution of *Pristinicola hemphilli* (squares) and *Taylorconcha serpenticola* Hershler, Frest, Johannes, Bowler & Thompson, gen. et sp. nov. (triangles). Symbols may refer to more than one locality.

are springs along the north side of the Snake River Canyon wall in the presumed vicinity of all five probable ferry sites, and a few springs on the south side as well. Specimens from two such sites (USNM 874426, USNM 874627) closely resemble the type material.

Distribution: Lower Snake-Columbia River basin of Idaho, Oregon, and Washington; minor Pacific Coastal drainages of Washington (Figure 7).

Ecology: *Pristinicola hemphilli* is found in permanent cold springs and strongly spring-fed creeks; in both cases most often near the source. These snails are generally absent from larger springs, often are highly abundant in very small spring seeps, but vary widely in occurrence and abundance among spring types. Animals sometimes occur in only one of an identical-appearing set of springs, or will be abundant in one and rare in adjacent sites of similar size, flow, substrate, etc. Frequently the snail will only

occur in one of several sets of springs found in a particular drainage.

This species usually lives on cobbles, but may also be found on rock faces. The substrate lithology generally is basalt. Snails are rarely found on mud, silt, plant debris, or living epiphytes. In a few cases, they were found in interstitial habitat among gravel, mostly in small springs with little flow. The animals appear to be strongly photophobic.

This species appears to have an annual cycle, with most adults dying off in late winter-early spring (after egg-laying) regardless of weather conditions. Newly hatched juveniles begin to appear in April, and are most common during this or the next month. Eggs are laid singly in very small capsules, often attached to sheltered sides or undersides of cobbles.

This species mostly lives in association with *Pisidium* (*Neopisidium*) *insigne*; *Fossaria* (*B.*) *dalli* also is often pres-

ent. In the Columbia Gorge, the snail tends to be absent from springs in which pleurocerid snails and/or *Lyogyrus* cf. *greggi* are abundant.

Remarks: Typically, the shell is elongate (SL/SW, 2.4), with a tapered apex, and aperture height about one-third shell height (Figure 2a, d-i). However, shells from a few populations in the Washington-Oregon Blue Mountains and from nearby western Idaho are relatively low and broad, with a blunt apex and aperture more than one-third shell height (Figure 2b, c). Mature size (shell height) also varies from population to population, even when adults with identical whorl numbers are compared (e.g., Figure 2f, h); and in a few samples, adult size was bimodal. (Note, in this regard, that we did not evaluate sexual dimorphism in shell size or shape.)

Pristinicola hemphilli has an unusually broad distribution among western American hydrobiids. Most sites are in Columbia Basin tributaries or immediately adjacent drainages, a region in which other hydrobiid genera (*Aminicola*, *Fluminicola*, *Lyogyrus*, *Pyrgulopsis*) are present but represented by few species. The genus appears to be absent from the Columbia drainage in northern Washington and Idaho. Known sites are south of the area in these states strongly affected by Late Pleistocene (Wisconsinan) glaciation. As yet, there are no sites in the Coast ranges or Rocky Mountains. *Pristinicola* is also absent from the Snake River Plain, i.e., the area occupied by Pliocene Lake Idaho, but present in the lower Snake system, which is believed to have been a part of the Columbia drainage since at least the Miocene. Most of the region of snail occurrence is comparatively young geologically. It is underlain by Miocene-Pliocene Columbia River Group flood basalts, and in great part was subjected to severe scour from the Pleistocene Lake Missoula Floods. Dispersal thus has likely been comparatively recent.

There is no fossil record for this genus either within its present distribution or in Lake Idaho sediments. A possibly related form occurs in the Eocene Princeton Group of British Columbia (*Micropyrgus camselli* Russell, 1957); and somewhat similar shells have also been noted from poorly preserved material from the Cretaceous Fort Union Group of North Dakota (*Micropyrgus minutulus* Meek, 1876) and the Oldman Formation (Cretaceous) of southern Alberta (*Hydrobia higdoni* Russell, 1937).

Material Examined:

IDAHO. Adams County: ANSP 82343, spring at Council (Washington County [now Adams County]; ANSP 82368, Price Valley, Weiser Canyon; USNM 874184, Unnamed spring, Price Valley, about 4.8 km northwest of HWY 95, sec. 12, T. 19 N, R. 1 W (used for anatomical description); USNM 874445, unnamed springs just south of Hells Canyon Dam, on east side of river, NE ¼ sec. 21, T. 22 N, R. 3 W. Idaho County: USNM 874425, Logged-Up Springs, Phillips Ridge, above Cow Creek, NE ¼ sec. 6,

T. 25 N, R. 1 E. Valley County: mountain near Big Payette Lake [now called Payette Lake, near McCall].

OREGON. USNM 531057. Baker County: USNM 874410, Mammoth Spring at Mammoth Spring Campground, Elk Creek, off FS2640, SE ¼ sec. 30, T. 13 S, R. 36 E; USNM 874422, Horse Spring, South Sister Creek, just south of Oregon Campground, on US 26, NE ¼ sec. 7, T. 12 S, R. 36 E. Grant County: USNM 874429, Big Springs, SW ¼ sec. 1, T. 12 S, R. 35 E; USNM 874430, unnamed spring above Clear Creek, on Clear Creek Road (FS147), SE ¼ sec. 10, T. 12 S, R. 35 E. Hood River County: USNM 874419, springs west of Oxbow Salmon Hatchery, NE ¼ sec. 7, T. 2 N, R. 8 E; USNM 874437, unnamed roadside spring east of Columbia Gorge Work Center, NW ¼ sec. 4, T. 2 N, R. 8 E. Jefferson County: USNM 874412, Opal Springs, northernmost spring, along Crooked River, NE ¼ sec. 33, T. 2 S, R. 12 E. Lane County: USNM 758255, South Fork McKenzie River, about 15 miles southeast of town at McKenzie Bridge. Multnomah County: USNM 854174, base of waterfall from unnamed creek, Pillars of Hercules, SE ¼ sec. 21, T. 1 N, R. 5 E; USNM 874411, unnamed spring east of Wahkeena Falls, on south side of railroad tracks, Benson State Park, SE ¼ sec. 12, T. 1 N, R. 5 E; USNM 874418, unnamed spring in gully east of Bridal Veil Creek, SE ¼ sec. 22, T. 1 N, R. 5 E; USNM 874427, unnamed spring adjacent to Bridal Veil Creek, NW ¼ sec. 25, T. 1 N, R. 5 E; USNM 874435, Bridal Veil Creek to south of bridge on east side of creek, NW ¼ sec. 26, T. 1 N, R. 5 E; USNM 874447, Wahkeena Creek, Columbia Gorge. Sherman County: USNM 854176, Frank Fulton Canyon, 2nd alcove on south side, east side spring complex, SE ¼ sec. 19, T. 2 N, R. 16 E; USNM 874438, Helms Springs, Helms Canyon, SW ¼ sec. 35, T. 3 N, R. 17 E; USNM 874439, small unnamed spring west of Biggs Junction, SW ¼ sec. 18, T. 2 N, R. 16 E; USNM 874442, unnamed side spring in Scott Canyon, south of Rufus, NE ¼ sec. 5, T. 2 N, R. 17 E; USNM 874443, Frank Fulton Canyon, 1st alcove on south side, east spring, SE ¼ sec. 19, T. 2 N, R. 16 E; USNM 874446, unnamed spring at mouth of Fox Canyon (west side), SW ¼ sec. 32, T. 3 N, R. 18 E. Union County: USNM 874624, Hale Spring, Mt. Emily, Blue Mountains, NE ¼ sec. 8, T. 1 S, R. 38 E; USNM 874433, unnamed spring on NFD100, off Owlsley Canyon Road, SE ¼ sec. 18, T. 2 S, R. 38 E. Wasco County: USNM 854173, unnamed spring above Eightmile Creek, NE ¼ sec. 15, T. 1 N, R. 14 E; USNM 854177, Oak Springs, near site of Tuscan, SW ¼ sec. 17, T. 4 S, R. 14 E; USNM 854178, unnamed spring above Eightmile Creek, NE ¼ sec. 9, T. 1 N, R. 14 E; USNM 874415, unnamed spring tributary to Eightmile Creek, SW ¼ sec. 15, T. 11 N, R. 14 E; USNM 874423, unnamed spring above Eightmile Creek, NE ¼ sec. 9, T. 1 N, R. 14 E; USNM 874428, Mosier Springs, Mosier Creek, NE ¼ sec. 12, T. 2 N, R. 11 E; USNM 874440, unnamed spring tributary to Eightmile Creek, SE ¼ sec. 9, T. 1 N, R. 14 E.

WASHINGTON. ANSP 31176 (lectotype), ANSP 368405 (paralectotypes), near Kentucky Ferry; ANSP 123162, spring on headwaters of Palouse River, Spokane Plain. Asotin County: USNM 854538, spring in unnamed tributary to Steptoe Canyon on east side of Colton Road, NW $\frac{1}{4}$ sec. 4, T. 11 N, R. 45 E; USNM 874421, unnamed spring at USGS gauging station north of Heller Bar, Hells Canyon, NE $\frac{1}{4}$ sec. 12, T. 7 N, R. 46 E. Columbia County: spring above Tucannon River and west of Tucannon Road in unnamed tributary northeast of Camp William T. Wooten State Park, NW $\frac{1}{4}$ sec. 21, T. 9 N, R. 41 E. Grant County: USNM 874416, spring on east side of Lenore Lake, Grand Coulee, NW $\frac{1}{4}$ sec. 13, T. 23 N, R. 26 E; USNM 874626, springs tributary to Rocky Ford Creek at Trout Lodge Hatchery, NW $\frac{1}{4}$ sec. 16, T. 21 N, R. 27 E. Klickitat County: USNM 854175, unnamed spring west of Sam Hill Bridge, SW $\frac{1}{4}$ sec. 5, T. 27 N, R. 16 E; USNM 854180, unnamed spring and spring run in Brooks Memorial State Park, NE $\frac{1}{4}$ sec. 3, T. 5 N, R. 17 E; USNM 874413, unnamed spring complex along WA14 above John Day Dam, SE $\frac{1}{4}$ sec. 19, T. 3 N, R. 17 E; USNM 874417, unnamed spring tributary to North Luna Creek, adjacent to Oak Flat Road, SE $\frac{1}{4}$ sec. 13, T. 4 N, R. 17 E; USNM 874424, unnamed springs (4; collection from easternmost) west of Hood River Bridge, SW $\frac{1}{4}$ sec. 24, T. 3 N, R. 10 E; USNM 874432, unnamed spring and spring run tributary to Rock Creek, near Newell Road crossing, NW $\frac{1}{4}$ sec. 20, T. 4 N, R. 19 E. Pierce County: ANSP 89303, upper valley of Nesqually [sic: Nisqually] River near Ashford; USNM 854171, unnamed spring on east side (center) of Ohop Lake, above Ski Park Road, SE $\frac{1}{4}$ sec. 3, T. 16 N, R. 4 E. Skamania County: UF 45971, Government Mineral Springs, 14 miles north-northwest of Carson; UF 45976, Beaver Pond, 10 miles north-northwest of Carson; USNM 854172, unnamed spring east of Galligan Spring and adjacent to WA14, NW $\frac{1}{4}$ sec. 30, T. 3 N, R. 10 E; USNM 854179, Franz Road springs, easternmost spring above WA14, NW $\frac{1}{4}$ sec. 4, T. 1 N, R. 6 E; USNM 854181, Galligan Spring, run just east of base of cutoff road adjacent to WA14, NW $\frac{1}{4}$ sec. 30, T. 3 N, R. 10 E; USNM 874409, unnamed spring and run tributary to Woodward Creek, near Beacon Rock, NE $\frac{1}{4}$ sec. 35, T. 2 N, R. 6 E; USNM 874414, Franz Road springs, easternmost spring from railroad tracks to WA14, NW $\frac{1}{4}$ sec. 4, T. 1 N, R. 6 E; USNM 874420, unnamed spring on west side of WA14 at site of Cruzatt, NE $\frac{1}{4}$ sec. 11, T. 1 N, R. 5 E; USNM 874436, unnamed spring complex north of west end of Spring Creek National Fish Hatchery, adjacent to WA14, SW $\frac{1}{4}$ sec. 22, T. 3 N, R. 10 E; USNM 874441, unnamed spring tributary to Greenleaf Creek near WA14 bridge, T. 2 N, R. 7 E; USNM 874444, unnamed spring and run tributary to Greenleaf Creek at Moffett Springs Road bridge, T. 2 N, R. 7 E. Spokane County: USNM 874431, unnamed spring above Spokane River near Petit Road exit, adjacent to Spokane Falls Community College Bridge, NW $\frac{1}{4}$ sec. 12, T. 50

N, R. 43 E. Whitman County: USNM 874426, spring tributary to unnamed creek above Central Ferry along WA 127, NW $\frac{1}{4}$ sec. 23, T. 14 N, R. 40 E; USNM 874627, spring on west side of Penawawa Road along unnamed creek tributary to Snake River, SE $\frac{1}{4}$ sec. 11, T. 14 N, R. 40 E.

Taylorconcha

Hershler, Frest, Johannes, Bowler & Thompson,
gen. nov.

Type species: *Taylorconcha serpenticola* sp. nov.; monotypy.

Etymology: Latin *concha*, shell (Feminine). Honoring Dwight Taylor, for his discovery and early work on this genus and, more generally, in recognition of his lifetime of fieldwork and research on the systematics, biology, and biogeography of the freshwater molluscan fauna of western North America. The common name, Bliss Rapids Snail, has been used for this taxon (Taylor, 1982; USDI, 1984, 1990, 1991a, b, 1992).

Diagnosis: Shell small to medium-sized, globose to ovate-conic, smooth, whorls slightly convex, with umbilicus small or absent. Aperture large, simple; inner lip usually incomplete. Protoconch about 1.5 whorls, lined with fine spiral lines. Operculum horny, paucispiral, attachment scar margin thickened along a portion of its length; attachment scar callus variably developed. Radula elongate, with central teeth having a single pair of basal cusps; cusp formula of central teeth, (4-5)-1-(4-5); lateral teeth 2-1-(2-3). Stomach without posterior appendix and with single opening to digestive gland. Cephalic tentacles ciliated with two to three narrow, longitudinal bands. Penis elongate-vermiform, without accessory lobes or glands. Female capsule gland with enclosed ventral channel and two distinct glandular zones. Bursa copulatrix absent.

Remarks: Unusual features of this genus include the elongate radula, weakly developed anterior pedal mucous gland, and absence of female bursa copulatrix, which is unique among North American hydrobiids, with the exception of several minute, highly reduced cave snails.

Taylorconcha serpenticola

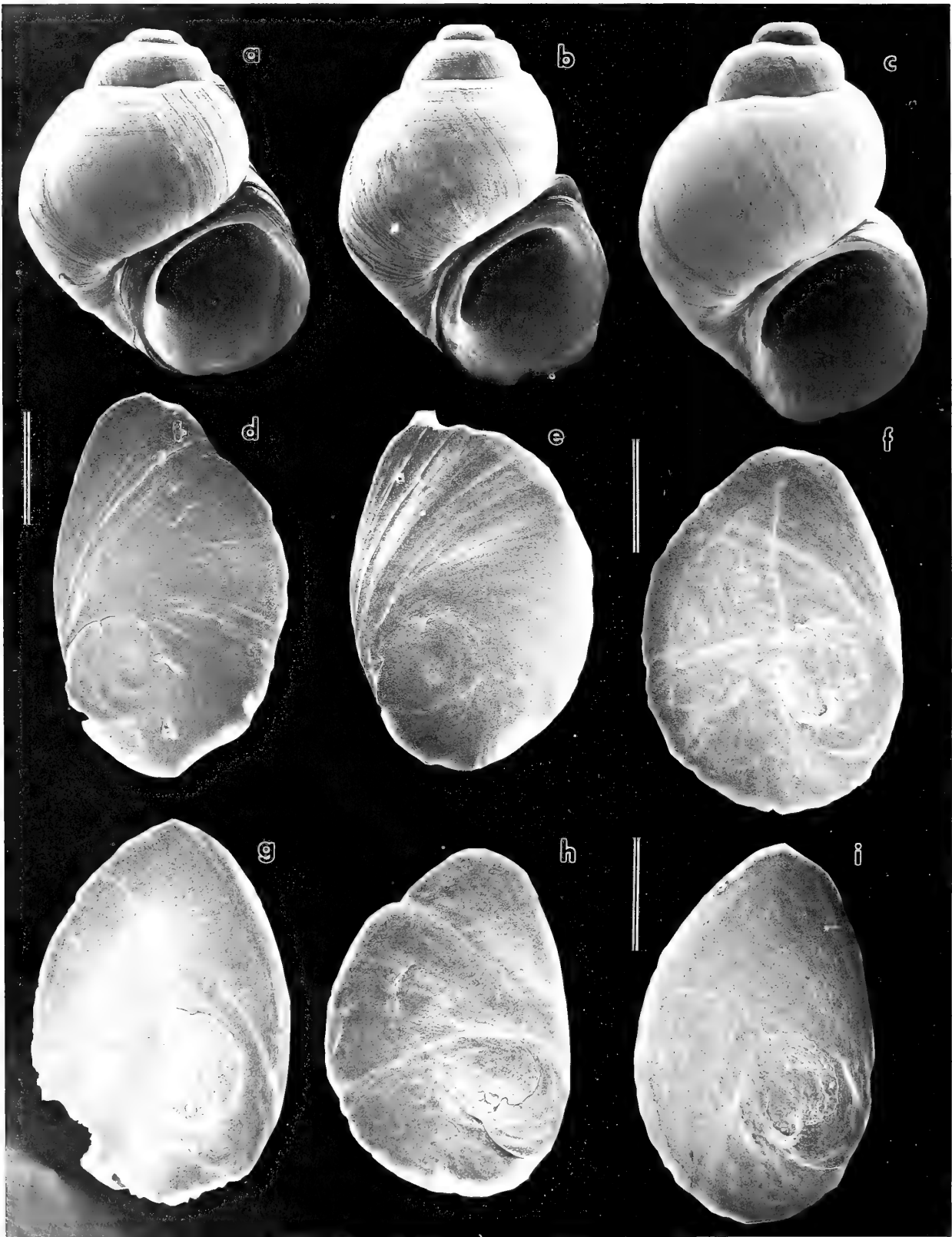
Hershler, Frest, Johannes, Bowler & Thompson,
sp. nov.

(Figures 1 [bottom row], 7-12)

Bliss Rapids Snail. Taylor, 1982:1. Bowler, 1991:175. Langenstein & Bowler, 1991:185. Bowler & Frest, 1992:30. Frest & Bowler, 1992:45. Frest & Johannes, 1992:16. Frest & Johannes, 1993a:5. Frest & Johannes, 1993b:5.

Genus and species undescribed [Bliss Rapids Snail]. USDI, 1984:21673. USDI, 1991b:58818.

Family Hydrobiidae, sp. nov. [Bliss Rapids Snail]. USDI, 1990:51931. USDI 1991a:50550. USDI 1992:59245.



Undescribed genus (Bliss Rapids Snail). Frest & Bowler, 1993:54.

Etymology: Latin *serpens*, snake, and *cola*, dweller; referring to the distribution of this species in the Snake River and associated springs.

Description: Shell (Figures 1 [bottom row], 8a–c) globose to ovate-conic; clear-white; length, 2.0–4.0 mm; total whorls, 3.5–4.5. Apex blunt; protoconch about 1.5 whorls, near planispiral; sculpture of numerous low spiral lines (Figure 9a, b). Teleoconch whorls slightly convex, with shallow sutures, sometimes strongly shouldered or with sub-sutural shelf. Teleoconch sculpture of strong collabral growth lines, usually accompanied by adapical striae. Aperture large, ovate, rounded below, slightly or strongly angled above. Inner lip complete in largest specimens, otherwise incomplete or a thin glaze; thickened, often greatly so adapically, slightly reflected; usually adnate, rarely slightly separated from body whorl. Outer lip thin to fairly thick, prosocline, often slightly sinuate. Umbilicus absent-small. Periostracum very light tan to dark brown-red. Shell measurements are in Table 2.

Operculum (Figure 8d–i) horny, thin, ovate, thin, light amber; nucleus eccentric; dorsal surface weakly frilled. Attachment scar margin thickened, sometimes broadly so, between nucleus and inner edge; sometimes also thickened along entire outer edge. Attachment scar callus small, weakly to rather strongly developed and raised.

Tentacle ciliation of two to three narrow longitudinal bands (Figure 9c–e). Distal tip of tentacle without elongate setae. Snout squat, near square; distal portion tapered, with well-developed lobes; tentacles stubby, considerably shorter than snout (in preserved material). Eyelobes absent. Foot near-circular, anterior end slightly convex, without lateral wings; posterior end slightly tapered, rounded. Anterior mucous gland very weakly developed, consisting of one or few very small, central units. Animal variably pigmented, ranging from pale except for black eyes to colored with epithelial black pigment as follows: tentacles darkened, especially along sides, except for distal tips; snout fairly light, with pigment heaviest on sides and distally; foot pale-light, with pigment mostly along anterior edge; opercular lobe pale-light, pigment mostly along inner edge; neck pale-very light; pallial roof and visceral coil dark, near-uniform.

Buccal mass medium-sized, extending from near base of tentacles to tip of snout; jaws present. Salivary glands

Table 2

Shell measurements of *Taylorconcha serpenticola* Hershler, Frest, Johannes, Bowler & Thompson, gen. et sp. nov. WH, number of whorls; SL, shell length; SW, shell width; LBWL BW, length of body whorl; AL, aperture length; AW, aperture width.

	WH	SL	SW	LBW	AL	AW
Holotype	3.5	2.45	1.78	2.16	1.31	1.09
Paratypes, <i>n</i> = 9						
Mean	3.5	2.32	1.82	2.07	1.25	1.15
SD	0.0	0.12	0.13	0.12	0.07	0.05
USNM 874590, <i>n</i> = 10						
Mean	3.75	2.93	2.08	2.42	1.41	1.32
SD	0.29	0.39	0.14	0.27	0.12	0.09

narrow, twisted, short, extending only to cerebral ganglia. Dorsal folds of esophagus simple.

Radular ribbon elongate, about 0.12 × 1.8 mm, with several coils alongside esophagus behind buccal mass, with about 115 rows of teeth. Central radular tooth (Figure 10a, b) broadly trapezoidal, with straight dorsal edge. Lateral angles short, strongly curved, strongly differentiated from tooth face by prominent neck. Basal process medium-broad; basal sockets deep. Central cusp pointed, up to twice as long as lateral cusps; lateral cusps, four to five. Basal cusp single, minute, arising from intersection between tooth face and lateral angle. Lateral tooth (Figure 10c–e) with broad central cusp flanked by two inner cusps and two to three outer cusps; cusps pointed. Basal cusp of lateral tooth well developed; lateral wing about one and half times as long as cutting edge. Marginal teeth (Figure 10c–f) with small, narrow cusps (inner tooth, 20–22; outer, about 25); lateral wings absent on teeth.

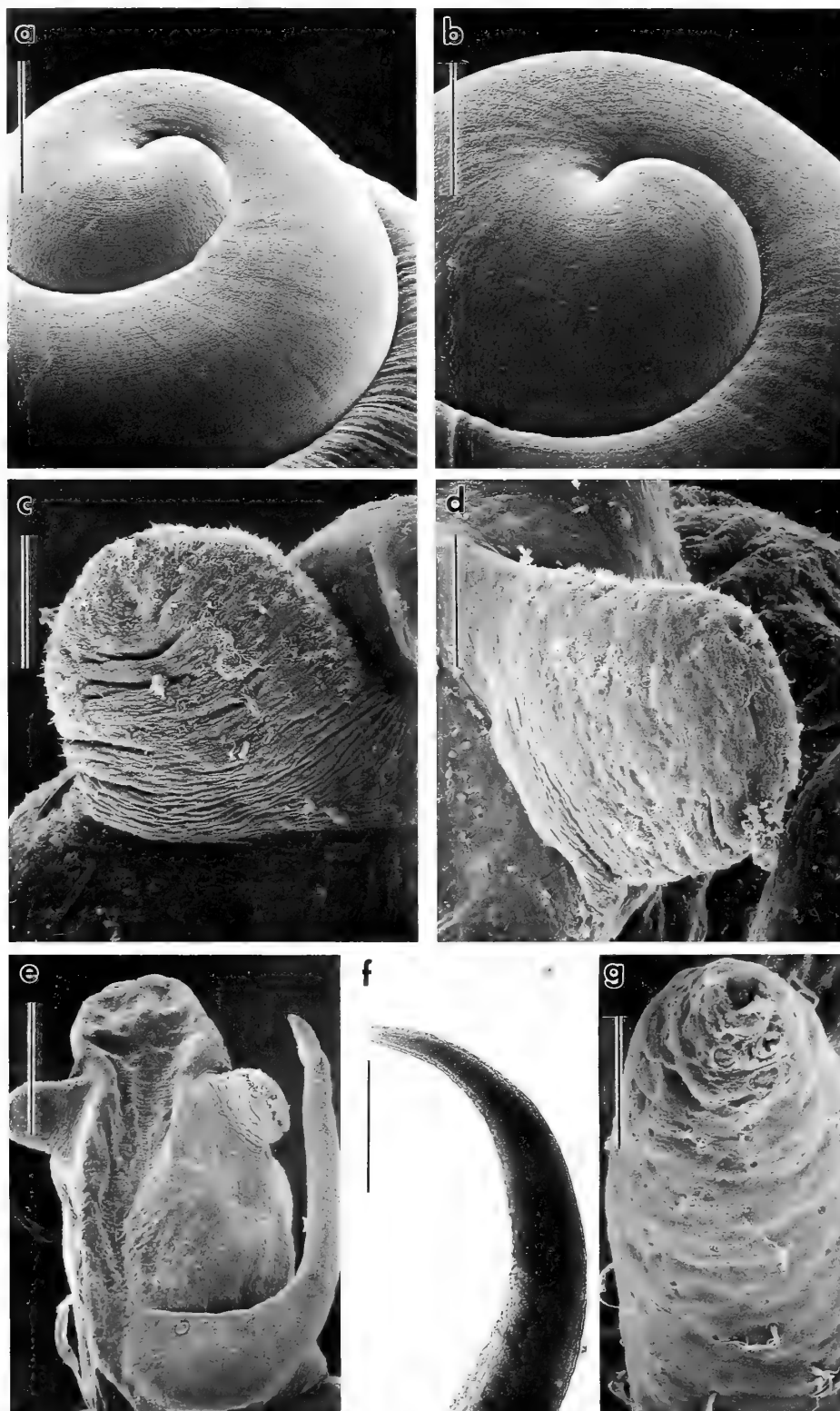
Stomach chambers about equal in length; posterior appendix absent. Stomach about one and half times as long as style sac, with single opening to digestive gland. Rectum without arch in pallial cavity; fecal pellets oriented longitudinally. Anus positioned near mantle edge, anterior to anterior end of capsule gland.

Mantle edge simple. Organs and structures of pallial cavity shown in Figure 11a. Ctenidium extending to slightly posterior to mantle edge; efferent vein short. Filaments about 17, fairly well developed, short, slightly broader than high, with central apex. Osphradium narrowly ovate, po-

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Figure 8

Scanning electron micrographs of shells and opercula of *Taylorconcha serpenticola* Hershler, Frest, Johannes, Bowler & Thompson, gen. et sp. nov. a, b. Paratypes, USNM 874588, shell height (a), 2.2 mm. c. USNM 874591. d, e. Dorsal operculum, USNM 874588, bar = 0.27 mm. f–i. Ventral operculum, USNM 874588, bars = 250 μm, 0.27 mm, 0.30 mm. Photographs of shells are printed to the same scale. e is printed to the same scale as d; g is printed to the same scale as f; h is printed to the same scale as d.



sitioned slightly anterior to middle of ctenidial axis. Hypobranchial gland with well-developed folds, especially anteriorly, but fairly thin. Kidney with slightly less than third of length in pallial roof. Renal gland very weakly developed, longitudinal. Renal aperture small, whitened. Body space with little connective tissue.

Testis, 0.75 whorl, composed of few broad lobes connected ventrally by vas efferens. Testis filling about half of length of visceral coil behind stomach and overlapping posterior stomach chamber. Vas deferens exiting from ventral testis about quarter of length posterior from anterior tip. Seminal vesicle a large mass underneath anterior third of testis. Prostate gland of complex histology, small, thin, ovate, with entire length posterior to pallial cavity wall, elongate oval in section; wall of medium thickness all around; lumen narrow, simple. Pallial vas deferens exiting from ventro-right lateral side slightly behind anterior end of prostate gland. Pallial vas deferens simple, embedded in connective tissue on pallial roof; anterior section simple, on pallial floor in connective tissue.

Penis (Figures 9e–g, 11b) originating near midline of neck, well behind tentacles; elongate-vermiform, tapering along entire length; large relative to head. Basal portion slightly expanded; penis without folds, but longitudinally striated (Figure 9f). Distal tip of penis tapering. Penial duct near straight; opening terminal, simple (Figure 9g). Distal penis with scattered bunches of cilia.

Ovary small, orange sac of less than 0.25 whorl containing about six oocytes, positioned behind the stomach and filling less than a quarter of the visceral coil behind the stomach. Distal female genitalia shown in Figure 11c. Glandular oviduct of complex histology. Capsule gland simple, shorter than albumen gland, composed of short, yellow posterior section and whiter anterior section. Lateral walls of capsule gland thick; ventral wall thin. Genital aperture small, subterminal pore borne on slightly raised papilla, without anterior vestibule. Albumen gland simple, greenish, with 20–25% of length in pallial roof. Coiled oviduct fairly small, thick, smooth, bound in connective tissue; composed of single, tight, circular-horizontal loop. Bursa copulatrix absent. Seminal receptacle filling 15–20% of albumen gland length; narrow, tubular; positioned obliquely on and shallowly imbedded in posterior half of albumen gland and extending to near posterior edge of gland. Lumen of seminal receptacle containing oriented sperm. Seminal receptacle duct poorly distinguished from

body, but of similar length and width, opening to oviduct at proximal end of coil near ventral edge of albumen gland.

Cerebral ganglia with spotted black pigment. RPG ratio about 23%; right pleural and supraesophageal ganglia weakly differentiated. Cerebral and pedal commissures elongate.

Type material: Thousand Springs (north springs), Gooding County, Idaho, SW $\frac{1}{4}$ sec. 8, T 8 S, R 14 E. Holotype, USNM 860583; paratypes, USNM 874588 (used for anatomical description), UF 194616.

Distribution: Historically known from a short reach of main stem Middle Snake River and associated springs, between Twin Falls and Indian Cove Bridge, Idaho (Figure 7). The highly disjunct, upstream record reported by Pentec Environmental, Inc. (1991) requires verification.

Ecology: *Taylorconcha serpenticola* occurs in both spring and riverine habitat. The snail is not found in impoundments, areas subject to major depth fluctuations, still or stagnant environments, lentic habitats, warm-water areas, typical river edge habitats, or areas with mud, sand, or fine gravel substrate. The species occurs only in flowing water, but is usually absent from whitewater areas. River populations now occur only in areas with strong spring influence, generally from springs emerging in the river bed. Such colonies tend to parallel river banks some distance from the normal low water mark, unless influx from bordering springs is present. We have found this taxon generally in water at 15–16°C.

Taylorconcha serpenticola is restricted to stable rocky substrates in areas with exceptional water quality. As most of the area inhabited by this snail has basalt as bedrock, lithologic preferences, if any, are uncertain. Taylor (1982) suggested that large cobbles and boulders with vesicular texture were preferred. We have found the snail on liths down to 1 cm in maximum dimension, with no apparent upper limit, and observed similar or even higher densities on smooth rocks compared to those with pumicelike textures. This species typically occurs only on the exposed lateral sides and undersides of rocks. The snails do not burrow in sediments, and are not found on rock surfaces in contact with soft sediment. Aside from occasional waifs, no live specimens were observed on mud or larger vegetation. Snails were found on well-secured deadwood, but

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Figure 9

Photographs and scanning electron micrographs of protoconch, head, and penis of *Taylorconcha serpenticola* Hershler, Frest, Johannes, Bowler & Thompson, gen. et sp. nov., USNM 874588. a, b. Protoconch, bars = 150 μ m, 120 μ m. c. Critical point dried left tentacle, bar = 75 μ m. d. Critical pointed dried right tentacle, bar = 86 μ m. e. Critical point dried head and penis, bar = 0.27 mm. f. Whole mount of distal penis, bar = 0.25 mm. g. Critical point dried distal tip of penis, bar = 17.6 μ m.

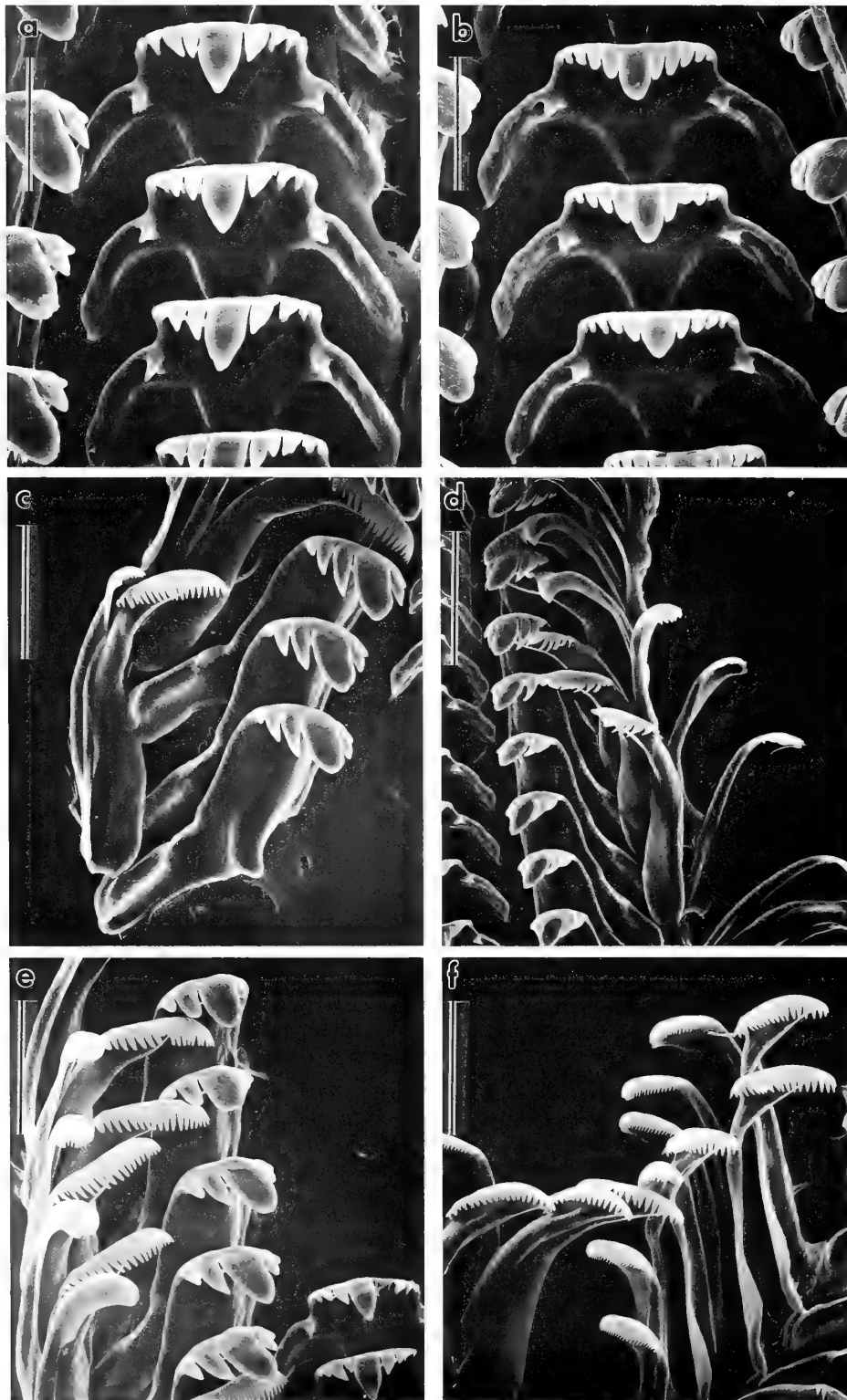


Figure 10

Scanning electron micrographs of radula of *Taylorconcha serpenticola* Hershler, Frest, Johannes, Bowler & Thompson, gen. et sp. nov., USNM 874588. a, b. Central radular teeth, bars = 15 μm , 17.6 μm . c-e. Lateral, marginal teeth, bars = 27 μm , 38 μm , 25 μm . f. Marginal teeth, bar = 27 μm .

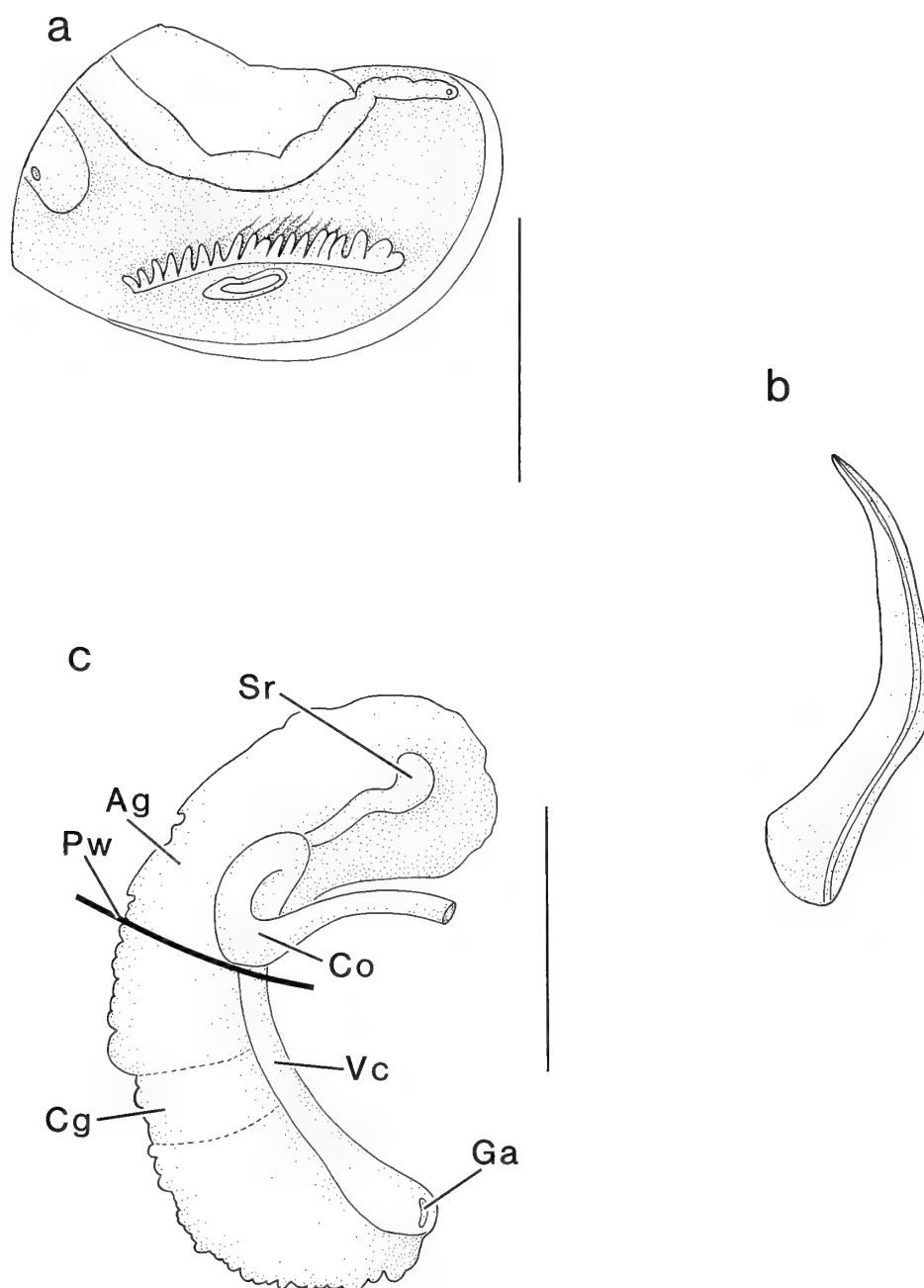


Figure 11

Anatomy of *Taylorconcha serpenticola* Hershler, Frest, Johannes, Bowler & Thompson, gen. et sp. nov., USNM 874588. a. Contents of pallial cavity, bar = 1.0 mm. b. Penis, scale as above. c. Distal female genitalia, left side, bar = 0.5 mm. Ag, albumen gland; Cg, capsule gland; Co, coiled oviduct; Ga, genital aperture; Pw, pallial wall; Sr, seminal receptacle; Vc, ventral channel.

seldom on loose pieces, and densities on any wood surface appeared quite low.

In spring-dwelling populations, egg laying apparently takes place from approximately December–March, while in the mainstream middle Snake River colonies, this occurs

in January and February. Eggs are laid singly, in very small capsules attached to the bottom or sides of rocks in protected areas also inhabited by adults. Eggs were not seen on the shells of living members of this or other local snail species. As with some other hydrobiids, most of the

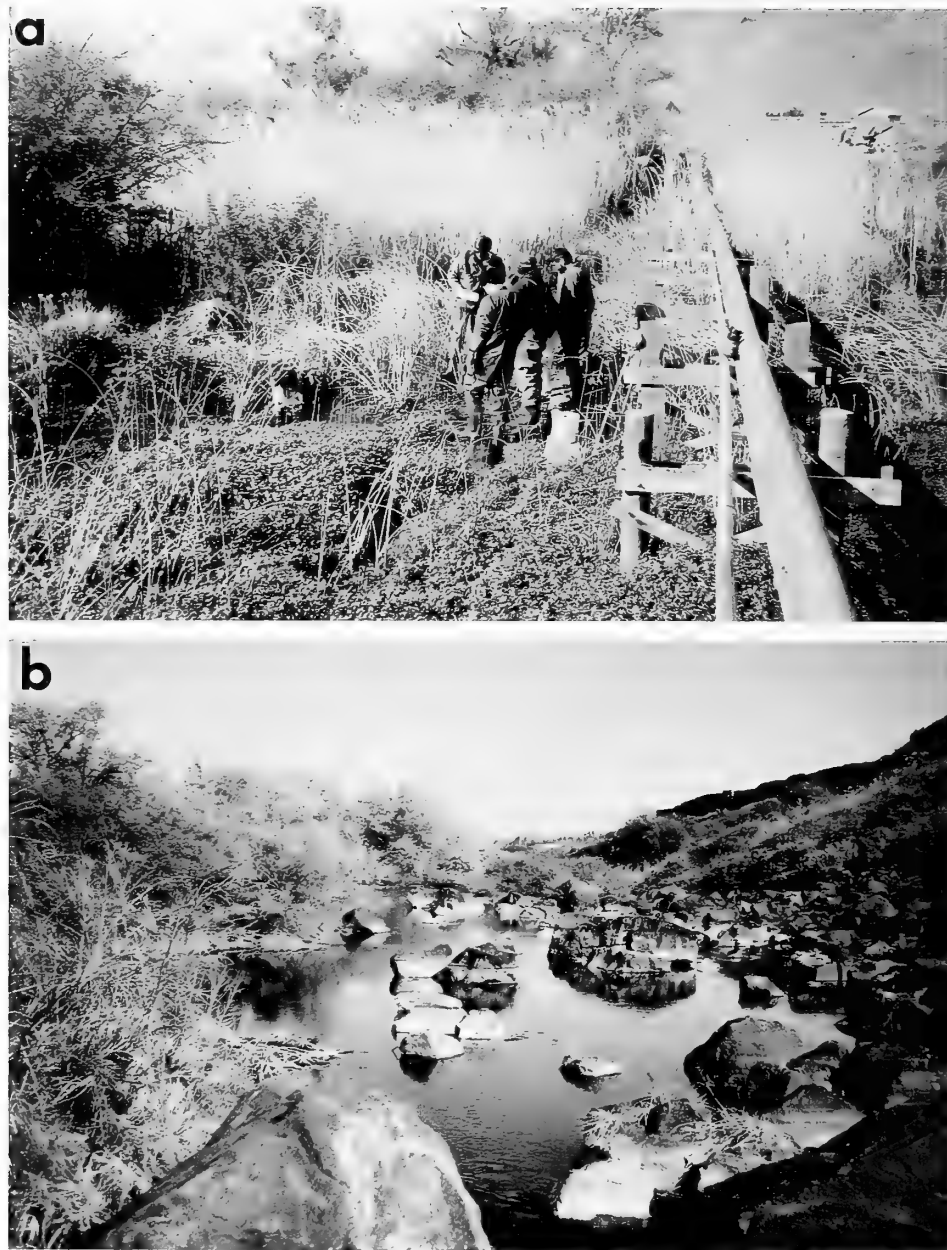


Figure 12

Photographs of Thousand Springs "North," Gooding County, Idaho, type locality of *Taylorconcha serpenticola* Hershler, Frest, Johannes, Bowler & Thompson, gen. et sp. nov. a. Upper portion of spring outflow, which is crossed by The Nature Conservancy pipeline. b. Lower portion of outflow.

adult population appears to be replenished annually, as particularly evident in the mainstem middle Snake River populations.

At relatively undisturbed sites, the most frequent associated mollusks are other cold-water forms such as *Fluminicola hindsi*, *Pyrgulopsis idahoensis*, *Vorticifex effusus*, *Physa natricina*, *Lanx* n. sp., and *Fisherola nuttalli* as well as *Physella* (*P.*) *gyrina*. *Taylorconcha serpenticola* is the

numerically dominant mollusk at most near-pristine sites: river localities now are often dominated by the introduced New Zealand mudsnail *Potamopyrgus antipodarum*. In many small spring or waterfall sites, our snail may be the only mollusk present.

Remarks: There are two morphs of *Taylorconcha serpenticola*. One (Figure 8a, b) has shells with orange-red

to pale orange periostracum, moderately convex whorls, fairly attenuate apex, strong collabral growth lines, thick parietal lip, and dark epithelial body pigment. The other morph (Figure 8c) has a nearly colorless shell, more rounded whorls, blunt apex, weak growth lines, thin parietal lip, and weaker body pigment in most populations. The two morphs may represent ecotypes, with the orange form typical of strongly spring-influenced mainstem colonies and relatively large springs, and the pale morph confined to mainstem river colonies with less obvious spring influence, and relatively shallow springs; but note that there are exceptions to these habitat generalizations. Most orange morph colonies occur in areas where encrusting red algae are common, suggesting that diet may be related to these color differences. The amount of shell variation in this snail does not exceed that recorded for several other western American hydrobiid species (e.g., *Pyrgulopsis micrococcus*: see Hershler & Sada, 1987; Hershler, 1989) and thus we only recognize a single taxon, although it would be desirable to obtain genetic data to further evaluate this problem.

Taylorconcha is known from the Late Pliocene (Blancan) Glens Ferry Formation, Gooding County; Early Pleistocene Bruneau Formation, Owyhee County; and from Late Pleistocene and probable Holocene deposits in Gooding County (Frest & Johannes, 1992), and is one of several surviving endemic relicts of Pliocene Lake Idaho or its Pleistocene successors. This lake formed as a result of tectonic activity in the Snake River Plain as early as 3.5 million years before the present (Y.B.P.) and persisted in some form into the Pleistocene, possibly to as late as 600,000 Y.B.P. Exact configuration of Lake Idaho changed through time, as a number of different Snake River Group basalt flows erupted during the lake's history, covering various areas of the Snake River Plain. However, the basic limits were approximately to the western Idaho–eastern Oregon border upstream from Hells Canyon and east to a point near American Falls, Idaho (Taylor, 1985; Malde, 1991). The mollusk fauna of Lake Idaho was exceptional and highly endemic, totalling over 80 taxa (Taylor *in* Malde & Powers, 1962; Taylor *in* Malde, 1972).

A few of the Lake Idaho endemics survive to the present. These occur only in a relatively short, unpolluted segment of the mainstem Snake River and in the extensive alcove spring complexes in the same reach. Increasing human settlement and activities have reduced the mainstem occurrences of these mollusks to a few isolated populations found mostly in a 38 km segment of the Snake River (the Wiley Reach, Hagerman Reach, and adjacent areas), and to a few populations in the few relatively undisturbed alcove spring complexes. The type locality of *Taylorconcha serpenticola* (Thousand Springs Preserve) is one of the best remaining examples. Water quality in the middle Snake River drainage has declined drastically in recent years, due to effects of irrigation, aquaculture, dairy farms, and hydroelectric projects, as well as increasing upstream irrigation, and urban usage and development (USDI, 1992).

Such considerations led Taylor (1982) to encourage federal listing of the snail as Endangered in his status report. After much further study (see Frest & Johannes, 1992, 1993b), the species was listed as Threatened (USDI, 1992).

In the last five years, new threats to the survival of *Taylorconcha* and other middle Snake River endemics have developed. The most important of these involves the parthenogenic New Zealand hydrobiid snail *Potamopyrgus antipodarum* (also known as *P. jenkinsi*), which was introduced into the Idaho Snake system in, or just subsequent to, 1985 and is now present in enormous numbers in the Snake River from at least Twin Falls to C. J. Strike Reservoir. By 1987, *P. antipodarum* had begun to invade the alcove springs, including the Thousand Springs Preserve (Taylor, 1987; Bowler, 1991; Langenstein & Bowler, 1991; Frest & Johannes, 1992). As yet, the species has had limited effects on *Taylorconcha* populations in springs. It is now the most abundant mollusk at river sites, and appears to negatively impact *Taylorconcha serpenticola*, minimally by crowding behavior during the frequent periods when peak loading at several hydroelectric dams affects the river. In the middle Snake River area, *P. antipodarum* is most successful in moderately polluted habitats and has made limited inroads into more pristine locales. This species has also invaded and spread throughout southern Australia and parts of western Europe (Ponder, 1988a).

Material Examined:

IDAHO. Elmore County: USNM 874590, Snake River at Clover Creek inflow, SW ¼ sec. 8, T. 5 S, R. 11 E; USNM 874591, USNM 874192, Snake River at Bancroft Springs, NE ¼ sec. 4, T. 6 S, R. 11 E. Gooding County: Thousand Springs, T. 8 S, R. 14 E: USNM 874463, USNM 874472, USNM 874491, USNM 874493, USNM 874496, Minnie Miller Lake and associated springs, NW ¼ sec. 8; USNM 874462, USNM 874478, Bridal Veil Springs, NW ¼ sec. 8; USNM 874503, USNM 874451, Minnie Miller Springs, second outlet springs, NW ¼ sec. 8; USNM 874466, USNM 874469, USNM 874473, USNM 874481, USNM 874483, USNM 874492, USNM 874502, USNM 874505, Minnie Miller Springs, first outlet springs, NW ¼ sec. 8; USNM 874467, USNM 874485, USNM 874487, USNM 874490, USNM 874494, USNM 874504, USNM 874592, Thousand Springs North Springs, SW ¼ sec. 8; USNM 874461, USNM 874464, USNM 874484, USNM 874489, USNM 874498, Sculpin Springs, SW ¼ sec. 17; USNM 874468, USNM 874501, springs below Sand Springs creek waterfall, SW ¼ sec. 17; USNM 874448, USNM 874482, USNM 874486, USNM 874488, USNM 874497, USNM 874510, Sand Springs Pool springs, SW ¼ sec. 17; Banbury Springs, NE ¼ sec. 33, T. 8 S, R. 14 E: USNM 874499, far north outlet; USNM 874477, fifth outlet south; USNM 874449, USNM 874471, USNM 874479, USNM 874495, mid-complex sites; USNM 874470, far south outlet; Box Canyon Creek, T. 8 S, R. 14 E; USNM 874474,

spring tributary to Box Canyon Creek on south side just above (east) of 1973 diversion pool, NE $\frac{1}{4}$ sec. 28; USNM 874475, just east of planned Hardy diversion, lower Box Canyon Creek, north side, NW $\frac{1}{4}$ sec. 28; USNM 874480, small alcove with spring just north of mouth of Box Canyon Creek on Snake River, NW $\frac{1}{4}$ sec. 28, T. 8 S, R. 14 E; USNM 874500, small alcove with spring above Malad River near junction with Snake River, NW $\frac{1}{4}$ sec. 35, T. 6 S, R. 13 E; USNM 874465, Niagara Springs at old public access to north of county access road, NE $\frac{1}{4}$ sec. 10, T. 9 S, R. 15 E; USNM 874586, Birch Creek, just below spring source, SE $\frac{1}{4}$ sec. 35, T. 6 S, R. 13 E. Twin Falls County: USNM 874450, Snake River on south side, about 180 m west of Bliss Bridge, subaqueous spring, SW $\frac{1}{4}$ sec. 7, T. 6 S, R. 13 E.

ACKNOWLEDGMENTS

We thank G. M. Davis and G. Rosenberg (ANSP) for lending specimens pertinent to this study. G. Steyskal (UF) provided valuable input pertaining to nomenclatural questions.

Scanning electron micrographs were taken by Susanne Braden of the NMNH (USNM) Scanning Electron Microscopy Laboratory, and prints of these were prepared by Victor Krantz (NMNH, Office of Printing and Photographic Services). Thin sections and whole mounts were prepared by B. Fricano. Maps and illustrations were prepared by M. Ryan (NMNH, Invertebrate Zoology) and S. Escher. Collecting permits were provided by Department of Fish and Game (State of Idaho). Partial support for fieldwork and laboratory studies was provided by the Smithsonian Institution Research Opportunities and Abbott Funds. We thank A. Kabat (NMNH), D. Lindberg (University of California, Berkeley), and W. Ponder (Australian Museum) for comments on the manuscript.

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New Species of Cypraeidae (Mollusca: Gastropoda) from the Miocene of California and the Eocene of Washington

by

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Abstract. Two new species of cypraeid gastropods are described from localities in Los Angeles County, California and Lewis County, Washington. *Zonaria* (*Zonaria*) *emmakingae* from the lower to middle Miocene ("Temblor Stage" = uppermost Burdigalian/Langhian), Topanga Canyon Formation is the earliest report of this genus and subgenus from the eastern Pacific region. *Nucleolaria* *cowlitziana* from the middle to upper Eocene ("Tejon Stage" = uppermost Bartonian/lowermost Priabonian), Cowlitz Formation is the earliest report of this genus worldwide and the only record of the genus from the eastern Pacific. Living species that are closely related to the two new species are also reviewed.

INTRODUCTION

Although the family Cypraeidae is well represented in the Cretaceous and much of the Cenozoic of the eastern Pacific (Ingram, 1947a, b; Groves, 1990, 1992), cypraeids are rare in Miocene deposits of California. Described herein is the first well-preserved cypraeid species from the Miocene of California. Generic and specific determinations cannot be made of the only previously reported cypraeids of the California Miocene: *Cypraea* n. sp. "A" from the Vaqueros horizon of Malibu Canyon and Santa Rosa Island, and *Cypraea* n. sp. "C" from the Temblor faunule of Topanga Canyon, southern California of Loel & Corey (1932). These poorly preserved internal molds superficially resemble the Recent Panamic species *Zonaria* (*Pseudozonaria*) *robertsi* (Hidalgo, 1906). The earliest appearance of *Zonaria* s.s. in the eastern Pacific is recorded here with the description of *Zonaria* (*Zonaria*) *emmakingae* Groves, sp. nov. from the lower to middle Miocene ("Temblor Stage" of Weaver et al. (1944) [= uppermost Burdigalian/Langhian]), Topanga Canyon Formation, Los Angeles County, southern California (Figure 1).

Also described herein is *Nucleolaria* *cowlitziana* Groves, sp. nov. from the middle to late Eocene ("Tejon Stage" of Clark & Vokes (1936) [= uppermost Bartonian/lowermost Priabonian]), Cowlitz Formation, Lewis County, Washington (Figure 1), the first Cenozoic cypraeid species described from Washington and the only record of the

genus in the eastern Pacific. The only other true cypraeid described from Washington is the Upper Cretaceous species *Palaeocypraea* (*Palaeocypraea*) *suciensis* (Whiteaves, 1895) from Sucia Island, San Juan Island (Groves, 1990).

The two new species here described represent the first appearances in the eastern Pacific of two lineages that have become diverse in the Recent fauna. This paper describes and figures these new species as well as illustrating and providing a brief synopsis of previously described, related species.

Abbreviations used for institutional catalogue and locality numbers are as follows: ANSP, Academy of Natural Sciences of Philadelphia; BMNH, The Natural History Museum, London; BPBM, Bernice P. Bishop Museum, Honolulu; CAS, California Academy of Sciences, San Francisco; LACM, Natural History Museum of Los Angeles County, Malacology Section; LACMIP, Natural History Museum of Los Angeles County, Invertebrate Paleontology; SDSU, San Diego State University; and UCMP, University of California Museum of Paleontology, Berkeley.

Measurement parameters are defined as follows: length = greatest distance between anterior and posterior ends; width = greatest distance between lateral margins; and height = greatest distance between base and dorsum.

The classification herein follows that of Schilder & Schilder (1971). The synonymies for the Recent species are limited to those with good illustrations or those that

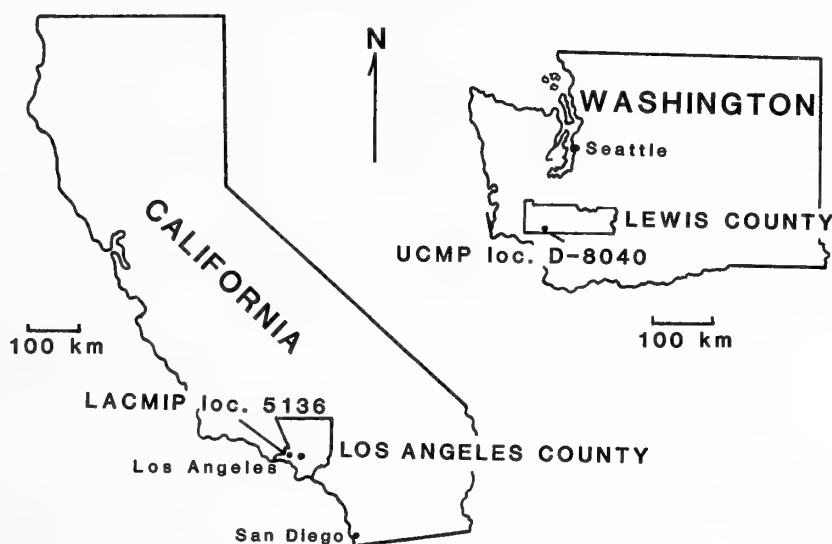


Figure 1

Index maps showing type localities of the new species of Miocene and Eocene cypraeids described herein. Localities are described in the "Localities Cited" section.

add pertinent taxonomic information. Citations of all fossil references are included in the synonymies and/or the stratigraphic distribution section, whether or not illustrated.

SYSTEMATIC PALEONTOLOGY

Superfamily CYPRAEACEA Rafinesque, 1815

Family CYPRAEIDAE Rafinesque, 1815

Subfamily ERRONEINAE Schilder, 1927

Tribe Zonariini Schilder, 1941

Genus *Zonaria* Jousseume, 1884

Subgenus *Zonaria* Jousseume, 1884

Type Species: *Cypraea zonata* Lamarck, 1810 (not Chemnitz, 1788) [= *Cypraea zonaria* Gmelin, 1791], by original designation. Recent, West Africa.

Diagnosis: Shell medium to large in size, pear-shaped; labial lip narrow, with teeth elongated; aperture straight, anteriorly curved toward columella; teeth on posterior canal weak; anterior columellar tooth oblique; fossula narrow with inner marginal teeth weak or absent; anterior and posterior canals deep; spire without furrow but commonly ribbed.

Remarks: *Zonaria* has been subdivided into *Zonaria* s.s., *Neobernaya* Schilder, 1927 [type species = *Cypraea spadicea* Swainson, 1823], and *Pseudozonaria* Schilder, 1927 [type species = *Cypraea arabicula* Lamarck, 1810]. *Zonaria* s.s. differs from *Z. (Neobernaya)* by its pear shape rather than

oblong shape, its lengthened anterior end, and stronger dentition. The fossula of *Zonaria (Pseudozonaria)* is denticulated and wider than in *Zonaria* s.s.

The earliest known species of *Zonaria* is *Z. (Z.) heilprinii* (Dall, 1890) from the lower Miocene (Aquitainian), Tampa Formation of Hillsborough County, Florida. West coast Miocene species of *Zonaria* ranged as far north as the central Santa Monica Mountains, Los Angeles County, California (at least 34°8'N) in the eastern Pacific (herein), Calhoun County, Florida (ca. 30°26'N) in the Caribbean (Dolin, 1991), and Torino, Piedmont Dist., Italy (ca. 45°5'N) in Europe (Schilder, 1932). The Recent Panamic *Z. (Z.) annettae* (Dall, 1909) ranges as far north as Laguna San Ignacio, Pacific coast of Baja California Sur, Mexico (ca. 26°44'N) and as far north as the head of the Gulf of California (ca. 31°37'N) (Burgess, 1985). *Zonaria (Z.) aequinoctialis* Schilder, 1933, the only other Panamic species of *Zonaria* s.s., ranges from Nicaragua to Peru (Burgess, 1985). The Recent *Z. (Z.) pyrum* (Gmelin, 1791) ranges as far north as the Mediterranean Sea in Europe (ca. 43°N) (Burgess, 1985) and is the only species of *Zonaria* from this region.

Zonaria s.s. disappeared from the Caribbean region in the late Miocene. The above mentioned Miocene northern ranges are similar to the Recent northern ranges of *Zonaria* s.s., and indicate similar climatic conditions for the Panamic and Mediterranean regions during the late early to middle Miocene. The presence of *Z. (Z.) emmalingae* and the associated warm-water gastropod genera *Nerita*, *Tonna*, and *Ficus* from the Topanga Canyon Formation indicate subtropical to tropical climatic conditions existed in what is now southern California (Susuki, 1951).



Explanation of Figures 2 to 5

Fossil and Recent species of *Zonaria* (*Zonaria*). Figures 2, 3. *Z. (Z.) emmakingae* Groves, sp. nov., holotype LACMIP 12277, from LACMIP loc. 5136, $\times 1.5$. Figures 4, 5. *Z. (Z.) annettae* (Dall, 1909), hypotype LACM 73-6.1, from LACM 73-6, $\times 0.9$.

Zonaria (*Zonaria*) *emmakingae* Groves, sp. nov.

(Figures 2, 3)

Diagnosis: A *Zonaria* s.s. with lengthened anterior, straight aperture; weak teeth on posterior canal; and smooth narrow fossula.

Description: Shell oblong, of medium size; spire covered; dorsum moderately arched; maximum height posterior of midpoint; aperture straight curving anteriorly toward columella; denticulation fine with smooth interstices; labial lip with 23 teeth; fossula smooth and narrow; basal marginal callus slight to moderate; terminal canals deep.

Type Materials: Holotype LACMIP 12277. The holotype measures 36.2 mm in length, 18.9 mm in width, and 17.2 mm in height.

Type Locality: LACMIP loc. 5136, central Santa Monica Mountains, Los Angeles County, southern California. The holotype was collected at the type section of the lower to middle Miocene ("Temblor Stage" = uppermost Burdigalian/Langhian), Cold Creek Member of Topanga Canyon Formation.

Arnold (1907:525-526) described a "Topanga Canyon fauna" at the head of Topanga Canyon, south of Calabasas, Los Angeles County, California. These outcrops were included in the type section of the Topanga Formation by Kew (1923:416-417), which he defined as middle Miocene marine exposures containing a "*Turritella coyana* fauna" overlying the Vaqueros Formation (lower Miocene) and underlying the Modelo Formation (upper Miocene). The type section of the formation consists of more than 2400 m of conglomerates, sandstones, and mudstones with intercalated basalts (Susuki, 1952). Yerkes & Campbell (1979) modified the formation name of Kew (1923) to the Topanga Canyon Formation of the Topanga

Group and described the Encinal, Saddle Peak, Fernwood, and Cold Creek members in the central Santa Monica Mountains. Flack (1990) reported the age of the Topanga Canyon Formation to be late early Miocene through middle Miocene, based on mollusks and benthic foraminifera.

Comparison: The new species is most similar to *Zonaria* (*Zonaria*) *annettae* (Dall, 1909:125) from the Pliocene through Recent of Baja California Sur and the Gulf of California. *Zonaria* (*Z.*) *emmakingae* differs from *Z. (Z.) annettae* by having a greater lateral extension of the labial lip, a greater number of labial teeth, and a basal marginal callus.

Discussion: Post-depositional lateral crushing has concealed the columellar lip dentition of the holotype, which is the only known specimen of the new species. Generic and subgeneric assignments, therefore, are based on the straight aperture, the smooth narrow fossula, and the pear shape. *Zonaria* (*Z.*) *emmakingae* is the earliest species of the genus and subgenus from the eastern Pacific.

Etymology: The new species is named after Mrs. Emma L. King, Manhattan Beach, California, active member of the Southern California Paleontological Society, who found the holotype in 1973 and graciously donated it to LACMIP.

Zonaria (*Zonaria*) *annettae* (Dall, 1909)

(Figures 4-5)

- Cypraea ferruginosa* Kiener, 1843-1845:37-38, pl. 56, fig. 3.
Not *Cypraea ferruginosa* Gmelin, 1791.
Cypraea sowerbyi Kiener, 1843-1845:38-39, pl. 7, fig. 3 [as *C. zonata*]; Reeve, 1845: pl. 10, sp. 40. Not *Cypraea sowerbyi* Gray, 1832; not Anton, 1839.
Cypraea annettae Dall, 1909:125; Durham, 1950a:116, pl.

30, figs. 7–8; Ingram, 1951:142–143, pl. 23, figs. 9–10; Cate, 1961:112–114, pl. 94, figs. 1–2b; Burgess, 1970:347, pl. 42, fig. A; Walls, 1979:246, 2 unnumbered figs.; Burgess, 1985:102, 3 unnumbered figs.

Zonaria annettae (Dall, 1909): Smith, 1944:21, fig. 249; Schilder, 1958:83–85, fig. 4b.

Zonaria (Zonaria) annettae annettae (Dall, 1909): Cate, 1969:113, pl. 12, figs. 9–11.

Zonaria annettae annettae (Dall, 1909): Allan, 1956:66, pl. 8, figs. 31–32; Lorenz & Hubert, 1993:117, pl. 61, figs. 1–9.

Cypraea (Zonaria) annettae Dall, 1909: Keen, 1958:330, fig. 287; Abbott, 1974:150, fig. 1642; pl. 5, fig. 1642.

Cypraea (Zonaria) annettae annettae Dall, 1909: Emerson & Old, 1963:12–14, fig. 14; Keen, 1971:495, fig. 933.

Type Material: The primary type material of *Cypraea ferruginosa*, *C. sowerbyi*, and *C. annettae* was not located.

Type locality: Of *C. ferruginosa*, type locality unknown. Kiener (1845:38) listed the type locality of *C. sowerbyi* as “l’Océan Pacifique, les côtes de la Californie.” Allan (1956:66) cited California as the type locality of *C. annettae*.

Geologic range: Late Pliocene (“San Joaquin Stage” of Weaver et al. (1944) [= Piacenzian]) to Recent.

Stratigraphic distribution: PLIOCENE: Bahía Merquer, Isla del Carmen (Durham, 1950a; Emerson & Hertlein, 1964); Puerto Ballandra, Isla del Carmen (Emerson & Hertlein, 1964). PLEISTOCENE: Pacific Coast of Baja California Sur: Bahía Tortugas (Chace, 1956; Emerson & Old, 1963; Emerson, 1980; Emerson et al., 1981); Bahía Magdalena (Dall, 1918; Grant & Gale, 1931; Jordan, 1936). Gulf Coast of Baja California Sur: Bahía San Carlos (Emerson, 1959; Emerson & Old, 1963); Santa Rosalia (Grant & Gale, 1931); Punta Chivato (Durham, 1950a; Emerson & Old, 1963; SDSU loc. 2555); Mulegé (herein); Isla Coronado (Durham, 1950a; Emerson & Old, 1963; Emerson & Hertlein, 1964); Isla del Carmen (Durham, 1950a; Ingram, 1951; Hertlein, 1957; Emerson & Old, 1963); Loreto and Punta Escondido (Ingram, 1951); Isla Monserrate and Isla San Diego (Emerson & Hertlein, 1964); Punta Coyote (CAS loc. 48867); Isla Cerralvo (Emerson, 1960a; Emerson & Old, 1963); Los Frailes (CAS loc. 60496). Sonora: Punta Peñasco (Emerson & Old, 1963); Isla Tiburón (CAS loc. 55064); Bahía Bacochibampo (Ingram, 1951). HOLOCENE: Isla San Jose [shell midden] (Emerson, 1960b).

Recent distribution: Found throughout the Gulf of California and to Laguna San Ignacio, Pacific coast of Baja California Sur, Mexico (Burgess, 1985) and to Rocas Alijos (LACM 90–119.4).

Remarks: The figured specimen (LACM 73-6.1) measures 42.8 mm in length, 22.9 mm in width, and 19.0 mm in height, and is from Punta San Antonio, northwest of Bahía San Carlos, Guaymas, Sonora, Mexico. *Zonaria (Z.) annettae* represents a modern descendant of *Z. (Z.) em-makingae*.

Subfamily EROSARIINAE Schilder, 1941

Tribe Erosariini Schilder, 1924

Genus *Nucleolaria* Oyama, 1959

Type Species: *Cypraea nucleus* Linnaeus, 1758, by original designation. Middle Miocene through Recent, Indo-Pacific.

Diagnosis: Shell small to medium in size; coarse to fine dorsal nodules with fine inter-nodular threads; prominent dorsal sulcus; coarse ventral ribs; fossula smooth and deep.

Remarks: Linnaeus (1758) described *Cypraea nucleus*, the first species of “rough cowry” from the Indo-Pacific. An endemic Hawaiian species, *Cypraea granulata*, was described by Pease (1862) as distinct from *C. nucleus*. Schilder (1937) described *Staphylaea (?) soloensis* from the Pliocene of Java and later reassigned it to the genus *Nucleolaria* (Schilder & Schilder, 1971). Burgess (1965) described *Cypraea cassiaui* from the Marquesas Islands, French Polynesia, and Flint and Starbuck Islands of the Line Islands, Kiribati. Schilder & Schilder (1971) assigned these related cypraeids to the genus *Nucleolaria* of Oyama (1959).

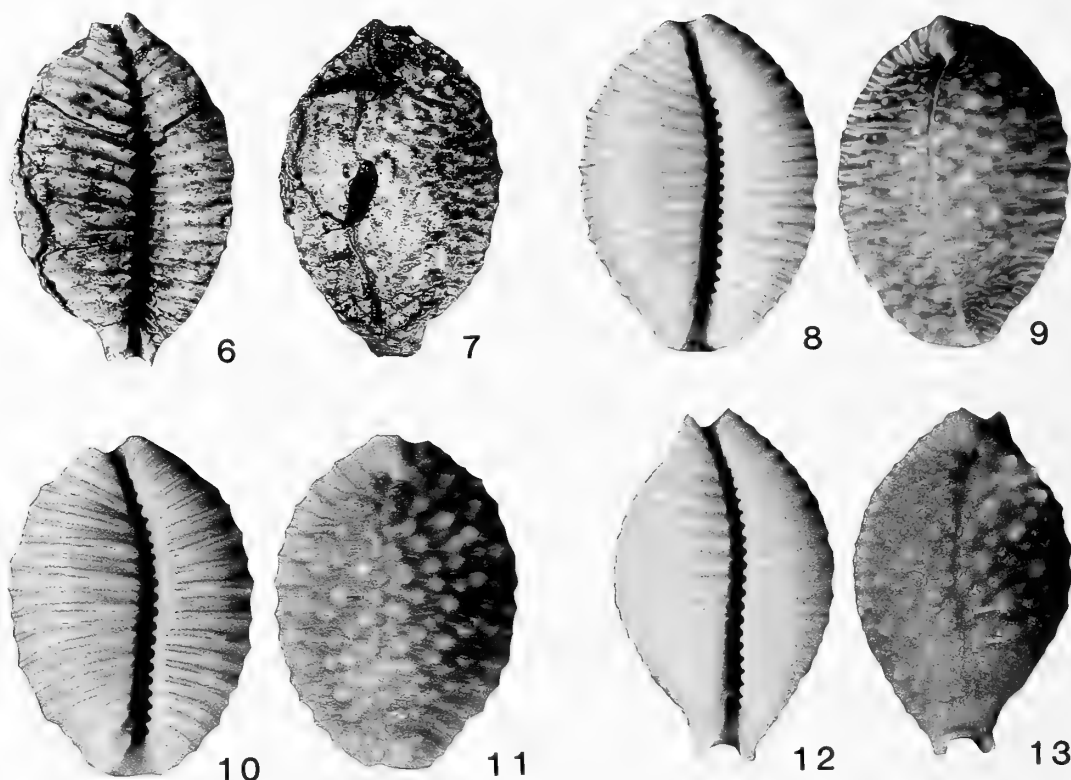
Nucleolaria is a tropical Indo-Pacific genus. The three living species *N. cassiaui* (Burgess, 1965) [Recent only], *N. granulata* (Pease, 1862) [Pleistocene to Recent], and *N. nucleus* (Linnaeus, 1758) [Miocene to Recent] and the Pliocene *N. soloensis* (Schilder, 1937) are known only from localities within the Indo-Pacific region. The new species of *Nucleolaria* described herein from the middle to late Eocene of southwestern Washington provides additional evidence that tropical conditions existed in this region. Durham (1950b) reported that the tropics extended northward of 49°N along the Pacific coast of North America during most of the Eocene. Squires & Groves (1993) also documented a middle Eocene tropical climate in King County, Washington by the presence of the ovulid species *Sulcocypraea mathewsonii* (Gabb, 1869) from the Tukwila Formation.

Nucleolaria cowlitziana Groves, sp. nov.

(Figures 6, 7)

Diagnosis: A *Nucleolaria* with prominent dorsal nodules connected by fine threads, a dorsal sulcus, and a deep fossula.

Description: Shell shape ovoid, medium in size; spire covered; maximum height slightly posterior of midpoint; dorsal groove faint; dorsal nodules smooth, circular, connected by fine threads that extend onto ventral surfaces and form prominent denticulation; slight marginal callus; aperture slightly curved posteriorly toward columella; denticulation prominent with smooth interstices, labial lip with 19 teeth, columellar lip with 18 teeth; fossula with strong denticulation; anterior and posterior canals prominently lengthened by terminal teeth.



Explanation of Figures 6 to 13

Fossil and Recent species of *Nucleolaria*. Figures 6, 7. *N. cowlitziana* Groves, sp. nov., holotype UCMP 39837, from UCMP loc. D-8040, $\times 1.6$. Figures 8, 9. *N. cassiaui* (Burgess, 1965), holotype BPBM 8910, from the Marquesas Islands, French Polynesia, $\times 1.5$. Figures 10, 11. *N. granulata* (Pease, 1862), hypotype LACM 149832, from Pokai Bay, Waianae District, Oahu, Hawaii, $\times 1.8$. Figures 12, 13. *N. nucleus* (Linnaeus, 1758), hypotype LACM 149833, from north of Auki, Malaita Island, Solomon Islands, $\times 2.1$.

Type Material: Holotype UCMP 39837. Represented only by the well-preserved holotype that displays original shell material and measures 27.2 mm in length, 17.3 mm in width, and 11.3 mm in height.

Type Locality: UCMP loc. D-8040, south-central Lewis County, Washington. The holotype was collected from type section of the middle to upper Eocene ("Tejon Stage" = uppermost Bartonian/lowermost Priabonian) Cowlitz Formation.

The Cowlitz Formation of Weaver (1912:11–14) was named for strata exposed 2.4 km (1.2 mi.) east of Vader, Lewis County, Washington, along the west bank of the Cowlitz River. Lithologies at the type section consist of thick-bedded, medium- to coarse-grained, brownish gray nearshore marine sandstone, as well as silty sandstone, sandy mudstone, estuarine and freshwater siltstones near the middle and intercalated basaltic flows near the base of the formation (Weaver, 1937). Nesbitt (1982) recognized three distinct faunal communities at the type locality: a *Turritella-Tivellina* community; a *Pitar* community; and a *Nuculana* community, which includes the new species of *Nucleolaria*.

Comparison: The new species is similar to the Recent *N. cassiaui* (Burgess, 1965:37–40, pl. 4, figs. E–H), *N. granulata* (Pease, 1862:278–279), and *N. nucleus* (Linnaeus, 1758:724). *Nucleolaria cowlitziana* differs from all three species by having a less prominent dorsal sulcus, finer dorsal nodules, a lower lateral profile, and stronger ventral ribbing. The ovulid species *Cypropterina* (*Jenneria*) *pustulata* (Lightfoot, 1786, ex Solander MS) lacks denticulation on the fossula.

Discussion: The excellent preservation allows for unequivocal generic assignment. *Nucleolaria cowlitziana* is significantly different from all other eastern Pacific cypræids and is the earliest member of this genus worldwide, as well as the only representative of the genus in the eastern Pacific region.

Etymology: The name refers to the Cowlitz Formation.

Nucleolaria cassiaui (Burgess, 1965)

(Figures 8, 9)

Cypraea cassiaui Burgess, 1965:38–40, pl. 40, figs. E–H; Burgess, 1970:37–38, pl. 1, fig. C; Burgess, 1985:234, 3

unnumbered figs.; Cook & Cook, 1992:5, 3 unnumbered figs.

Nucleolaria nucleus cassiaui (Burgess, 1965); Schilder & Schilder, 1971:66, 103.

Naria (*Nuclearia*) *granulata cassiaui* (Burgess, 1965): Cossignani & Passamonti, 1991:21, 41.

Staphylaea granulata cassiaui (Burgess, 1985): Lorenz & Hubert, 1993:216, pl. 101, figs. 30–31, 33–34.

Type Material: Holotype BPBM 8910; paratypes, ANSP 80860 and 80063. The holotype measures 29.4 mm in length, 17.5 mm in width, and 13.7 mm in height.

Type Locality: Marquesas Islands, French Polynesia (Burgess, 1965).

Geologic Range: Recent only.

Remarks: *Nucleolaria cassiaui* differs from other “rough cowries” by having a unique dorsal groove that is a trench-like slit, which is not encroached upon by the adjacent tubercles and threads.

Recent Distribution: This species is only known from the Marquesas Islands, French Polynesia, and Starbuck and Flint Islands in the Line Islands, Kiribati (Burgess, 1985).

Nucleolaria granulata (Pease, 1862)

(Figures 10, 11)

Cypraea granulata Pease, 1862:278–279; Kay, 1965:79–80, pl. 14, figs. 17–18; Kosuge, 1969:785, 789, pl. 4, fig. 60; Burgess, 1970:263–264, pl. 29, figs. I–J; Kay, 1979:193, frontis., third row; Walls, 1979:140, 2 unnumbered figs.; Burgess, 1985:236, 3 unnumbered figs.

Cypraea madagascarensis Gmelin, 1791: Kiener, 1843–1845: 126–127, pl. 3, fig. 4; Reeve, 1845: pl. 15, sp. 75; Sowerby, 1870:41, pl. 33, figs. 406–408. Not *Cypraea madagascarensis* Gmelin, 1791.

Cypraea honoluluensis Mevill, 1888:245.

Staphylaea (*Nuclearia*) *granulata* (Pease, 1862): Cate, 1965: 51–52, pl. 5, figs. 7a–b.

Staphylaea granulata (Pease, 1862): Morris, 1966:233, pl. 68, fig. 7.

Nucleolaria nucleus granulata (Pease, 1862): Schilder & Schilder, 1971:66, 119.

Naria (*Nuclearia*) *granulata* (Pease, 1862): Cossignani & Passamonti, 1991:21, 64.

Staphylaea granulata granulata (Pease, 1862): Lorenz & Hubert, 1993:215, pl. 101, figs. 19–29, 32.

Type Material: Kay (1965:80) selected a lectotype BMNH 1964306 and three paralectotypes BMNH 1964307. The lectotype was selected because it best represented the details of the description given by Pease.

Type Locality: “Sandwich Islands” (= Hawaiian Islands) (Sowerby, 1870).

Geologic Range: Pleistocene to Recent.

Stratigraphic Distribution: PLEISTOCENE: Oahu, Hawaii (Kosuge, 1969).

Recent Distribution: Limited to the Hawaiian Archi-

pelago from Kure Atoll to the Island of Hawaii and collected from Holocene deposits on Johnston Island in January, 1964 (Burgess, 1985).

Remarks: The figured specimen (LACM 149832, ex L. T. Groves coll.) measures 23.6 mm in length, 17.3 mm in width, and 10.9 mm in height and is from Pokai Bay, Waianae District, Oahu, Hawaii. *Nucleolaria granulata* is most similar to *N. cassiaui*, but the dorsal groove is less prominent in *N. granulata*.

Nucleolaria nucleus (Linnaeus, 1758)

(Figures 12, 13)

Cypraea nucleus Linnaeus, 1758:724; Kiener, 1843–1845:127, pl. 3, fig. 2; Reeve, 1845: pl. 15, sp. 70; Sowerby, 1870: 40, pl. 33, figs. 399–400; Woodward, 1879:497–498, pl. 13, figs. 7a–b; Vlerk, 1931:244; Kosuge, 1969:785, 793; Burgess, 1970:261, pl. 29, fig. H; Kay, 1979:197, figs. 68.C–D; Walls, 1979:205, 2 unnumbered figs.; Burgess, 1985:235, 3 unnumbered figs.

Cypraea madagascarensis Gmelin, 1791:3419; Ostergaard, 1928:6; Ostergaard, 1939:70, 72–73, 76.

Cypraea (*Pustularia*) *nucleus* Linnaeus, 1758: Ladd, 1945: 366, pl. 52, figs. Q–S.

Staphylaea (*Nuclearia*) *nucleus* (Linnaeus, 1758): MacNeil, 1960:51–52, pl. 19, figs. 5–6.

Staphylaea nucleus (Linnaeus, 1758): Cernohorsky, 1967:84, pl. 13, fig. 70.

Nucleolaria nucleus nucleus (Linnaeus, 1758): Schilder & Schilder, 1971:66, 138.

Cypraea (*Staphylaea*) *nucleus* Linnaeus, 1758: Ladd, 1977: 24, pl. 5, figs. 4–6.

Naria (*Nuclearia*) *nucleus* (Linnaeus, 1758): Cossignani & Passamonti, 1991:21, 90.

Nucleolaria nucleus (Linnaeus, 1758): Lorenz, 1992:28, pl. 10, figs. 104–105.

Staphylaea nucleus nucleus (Linnaeus, 1758): Lorenz & Hubert, 1993:214, pl. 101, figs. 1–3, 7–19, 13–15.

Staphylaea nucleus madagascarensis (Gmelin, 1791): Lorenz & Hubert, 1993:215, pl. 101, figs. 4–6, 10–12, 16–18.

Type Material: Type material not located.

Type Locality: Of *C. nucleus*, “l’océan des grandes Indes et la mer Pacifique” (Kiener, 1844:127); Ambon (= Amboina), Pulau Ambon, Indonesia (Allan, 1956). Of *C. madagascarensis*, “Madagascar et l’océan Pacifique” (Kiener, 1844:126).

Geologic Range: Middle Miocene to Recent.

Stratigraphic Distribution: MIOCENE: Nias Island, Indonesia (Woodward, 1879; Vlerk, 1931). PLIOCENE: Ndolithoni Formation, Vanua Mblavu Island, Fiji (Ladd, 1945; 1977). PLEISTOCENE: Yontan Limestone, Okinawa (MacNeil, 1960); Oahu, Hawaii (Ostergaard, 1928 [as *Cypraea madagascarensis*]; Kay, 1961; Kosuge, 1969); Molokai, Hawaii (Ostergaard, 1939 [as *Cypraea madagascarensis*]; Hurghada, Egypt (Lorenz, 1992).

Recent Distribution: Found throughout the Indo-Pacific (Burgess, 1985).

Remarks: The figured specimen (LACM 149833, *ex* L. T. Groves coll.) measures 22.2 mm in length, 19.0 mm in width, and 11.2 mm in height and is from Malaita Island, Solomon Islands. *Nucleolaria nucleus* is less ovate than the other "rough cowries" and has more prominent terminal extremities.

ACKNOWLEDGMENTS

The following persons generously helped in this project and are gratefully acknowledged. Edward C. Wilson (LACMIP) arranged for the loan of the Topanga Canyon Formation specimen, and LouElla R. Saul and George L. Kennedy (LACMIP) provided access to the Natural History Museum of Los Angeles County, Invertebrate Paleontology collection. Robert H. Cowie and Reggie K. Kawamoto (BPBM) loaned comparative material. David R. Lindberg (UCMP) loaned the Cowlitz Formation specimen. Elizabeth Kools and Jean DeMouthe (CAS) provided pertinent locality information. Mrs. Emma L. King collected the Topanga Canyon Formation specimen and graciously donated it to LACMIP. Mr. Charles R. King of the Redondo Gem and Mineral Society, Inc., arranged for a generous research grant. Richard L. Squires (California State University, Northridge) critically read the manuscript and gave valuable insights concerning eastern Pacific Eocene stratigraphy, chronology, and paleoclimate. Helga Schwarz-Chung (LACM Ichthyology) kindly translated parts of Wenz (1941). Jennifer L. Edwards and Donald W. McNamee (LACM Research Library) and Melinda Hayes, Suzanne Henderson, and Jean Crampon (Allan Hancock Foundation Library, University of Southern California) assisted in locating obscure and rare references. James H. McLean, (LACM) LouElla Saul (LACMIP), George L. Kennedy (SDSU), and two anonymous reviewers critically evaluated the manuscript and made valuable suggestions.

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- CAS loc. 48867. Raised beach at Punta Coyote, ca. 22 km northeast of La Paz, Baja California Sur, Mexico. Collector: A. G. Smith, 3 November 1954. Pleistocene.
- CAS loc. 55064. Lowest terrace ca. 30 m (100 ft.) from shore in a prominent bay directly north of Isla Turner, southeastern part of Isla Tiburón, Gulf of California, Mexico. Collector: T. Stump, 1974. Pleistocene.
- CAS loc. 60496. Sea-facing sandstone outcrop 3.2 km (2 mi.) southwest of Morro los Frailes and 49.8 km (31 mi.) northeast of San Jose del Cabo, Baja California Sur, Mexico, 23°22'N, 109°25'W. Collector: C. Baumbach, 8–9 July 1979. Pleistocene.
- LACM 73–6. Intertidal, rocky bar leading to Isla Venado, Punta San Antonio, northwest of Bahía San Carlos, Guaymas, Sonora, Mexico, 27°58'N, 111°07'W. Collectors: J. H. McLean & J. Margetts, 30–31 January 1973. Recent.
- LACM 90–119. 20–50 m depth (65–164 ft.), rocks and

pinnacles of Rocas Alijos, Pacific Coast Baja California Sur, Mexico, 24°57.59'N, 114°44.92'W. Collectors: R. Schmieder, M. K. Wicksten, and R. Van Syoc, R/V *Qualifier*, 31 October–7 November 1990. Recent.

- LACMIP loc. 5136. Exposures in prominent roadcut ca. 5.3 km (3.3 mi.) south of U.S. Highway 101 on south side of Old Topanga Road ca. 30 m (100 ft.) upslope from a conspicuous bed of turritellas in roadcut, NW¼ SW¼ sec. 35, T1N, R17W, SBBM, Malibu Quadrangle, Los Angeles County, California. Collector: E. L. King, 10 August 1974. Lower to middle Miocene ("Temblor Stage" = uppermost Burdigalian/Langhian), Topanga Canyon Formation.
- SDSU loc. 2555. Second and largest arroyo west of 1224 m (4000 ft.) runway, Punta Chivato, ca. 22.4 km north-east of Mulegé, Gulf of California, Baja California Sur, Mexico. Collector: J. L. Egan, April 1972. Pleistocene.
- UCMP loc. D-8040. Northwest bank of the Cowlitz River bend, down dirt road to city water pump facility, 2.4 km (1.5 mi.) east of Vader, SW¼ sec. 27, T11N, R2W, and center of NW¼ sec. 33, T11N, R2W, WBM, Castle Rock Quadrangle, Lewis County, Washington. Middle to upper Eocene ("Tejon Stage" = uppermost Bartonian/lowermost Priabonian), Cowlitz Formation.

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New Species of Early Eocene Small to Minute Mollusks from the Crescent Formation, Black Hills, Southwestern Washington

by

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Abstract. Seven new species of small to minute gastropods and one new species of a minute bivalve are reported from the early Eocene upper part of the Crescent Formation in the Black Hills west of Olympia, Washington. These species lived in a rocky intertidal environment where accumulation of basalt flows caused shoaling of marine waters. Their shells were deposited as the matrix of coquina that infilled cracks between individual eroded boulders of basalt, but the small size of the new species prevented them from being broken during transport. Associated macrofossils indicate a middle early Eocene age ("Capay Stage").

Description of these new species extends the geographic and chronologic range of each of the supraspecific taxa to which the species are assigned. The fissurellid *Emarginula washingtoniana* is the first reported Cenozoic species of this genus from the Pacific coast of North America. The trochid *Calliovarica pacifica* is only the second known species of this early Eocene genus and extends its geographic range from California into Washington. The skeneid *Haplocochlias montis* is the first positively known fossil species of *Haplocochlias* and the earliest known representative of family Skeneidae, whose previous geologic range was early Miocene to Recent. The neritid *Nerita* (*Theliostyla*) *olympia* is the first "Capay Stage" species of this subgenus from the Pacific coast of North America. The rissoid *Lapsigyrus crescentensis* is the earliest record of this genus, whose previous geologic range was Pleistocene to Recent. The columbellid *Mitrella* (*M.*) *blackhillsensis* is the earliest record of this genus, whose previous geologic range was early Miocene to Recent. The ellobiid *Ovatella* (*Myosotella*) *coneyi* is the first record of a marine pulmonate in the lower Tertiary of the Pacific coast of North America. The tellinid bivalve *Linearia* (*Linearia*) *louellasaulae* is the first confirmed species of this genus from the Pacific coast of North America and the youngest record of this genus, whose previous geologic range was Early to Late Cretaceous.

INTRODUCTION

Molluscan assemblages from the Eocene Crescent Formation in Washington have received little study. Nearly all of the previous reports deal with the Crescent Bay area along the north shore of the Olympic Peninsula (Figure 1). One of these reports is by Weaver & Palmer (1922), who described, named, and illustrated five species of gastropods and two species of bivalves. Recently, Squires et al. (1992) did a detailed study of the macrofossils of the upper Crescent Formation at Pulali Point in the eastern Olympic Peninsula just west of Seattle (Figure 1), and this study spawned two additional articles (Squires, 1992a, 1993) on certain bivalves from the Pulali Point area. More recently, Squires & Goedert (in press) have done a detailed study of the macrofossils of the upper Crescent Formation in the Little River area in the southern Olympic Peninsula (Figure 1).

The present study, which is a continuation of our investigation of the macrofossil faunas of the Crescent Formation in western Washington, differs from our previous studies in that many of the fossils are small to minute (i.e., less than 5 mm in longest dimension). Eocene small to minute gastropods and bivalves from the Pacific coast of North America are not well known. They easily become an integral part of the cement that holds a rock together and, in nearly every case, cannot be extracted for study. Previous investigations that included minute mollusks concern a part of the fauna found in the upper Eocene part of the Lincoln Creek Formation in the "Gries Ranch beds" in southwestern Washington (Effinger, 1938), a fauna from middle Eocene rocks in the Vacaville, northern California area (Palmer, 1923), and a part of the fauna found in the middle to upper Eocene Tejon Formation in south-central California (Anderson & Hanna, 1925). The present study area in the Black Hills of southwestern Washington has a more diverse gastropod assemblage than these other locales because, as will be discussed below, the study area contains a rocky intertidal assemblage that has been preserved nearly in place. Lindberg & Squires (1990) noted that rocky intertidal organisms are poorly represented in the pre-Pleistocene fossil record because they are usually swept away and broken up by wave action. The Black Hills assemblages, therefore, contain genera that are very rare in the fossil record due to two factors: their small size and their preference for a rocky intertidal habitat.

The molluscan stages used in this report stem from Clark & Vokes (1936), who proposed five mollusk-based provincial Eocene stages, namely, "Meganos," "Capay," "Domengine," "Transition," and "Tejon." The stage names are in quotes because they are informal terms. Givens (1974) modified the use of the "Capay Stage," and it is in this modified sense that the "Capay Stage" is used herein.

The classification system used for taxonomic categories higher than the family level generally follows that of Haszprunar (1988). Abbreviations used for catalog and/or lo-

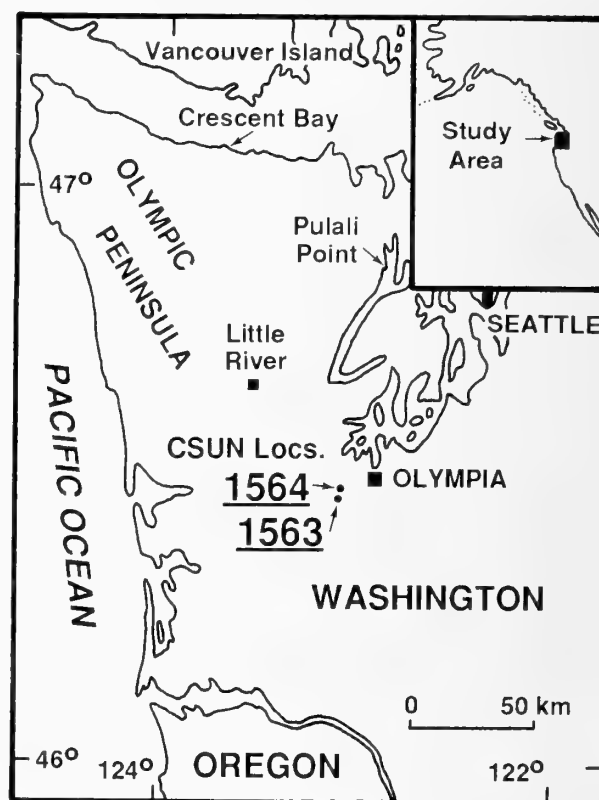


Figure 1

Index map to CSUN collecting localities, Crescent Formation, Black Hills area, west of Olympia, Washington.

cality numbers are: CSUN, California State University, Northridge; LACM, Natural History Museum of Los Angeles County, Malacology Section; LACMIP, Natural History Museum of Los Angeles County, Invertebrate Paleontology Section; UCMP, University of California Museum of Paleontology (Berkeley).

GEOLOGIC AND DEPOSITIONAL SETTING

The basement rock in the Olympic Peninsula of southwestern Washington is the upper Paleocene to lower middle Eocene Crescent Formation, which consists predominantly of oceanic tholeiite basalt flows. Several models have been proposed for the origin of these flows. Most of the early models, which are reviewed by Snively (1987), envisage accretion of seamounts, but in recent years, the models favor a rift-basin environment (Babcock et al., 1992). The upper third of the formation ranges from a deep-to-shallow marine environment to one that is locally terrestrial. Interbedded marine sedimentary rocks locally contain fossils, especially at places like Pulali Point and the Little River area where the extrusion of the basalt flows caused

shoaling of the marine waters (Squires et al., 1992; Squires & Goedert, in press).

About 15 km west of Olympia (Figure 1), in the Black Hills area in the Washington Coast Range, there is a > 600 m-thick sequence of basalt flows and breccias, with minor interbeds of basaltic sandstone and siltstone that are correlated with the Crescent Formation in the Olympic Peninsula (Globerman et al., 1982). The Black Hills is one of several large basement uplifts in the Washington Coast Range and is heavily forested with rock exposures generally limited to roadcuts and quarries. Macrofossils were found at only two localities in the Crescent Formation in the Black Hills. One of these is near Larch Mountain at CSUN loc. 1563, which is the same site that Pease & Hoover (1957) first noted, but their coordinates differ slightly. The other locality is about 3.5 km to the northeast and near Rock Candy Mountain at CSUN loc. 1564 (Figure 1).

At the Larch Mountain locality, there is a roadcut exposure of light-colored sedimentary rock interbedded with basalt. The exposure is 1 m thick and consists of an eroded vesicular basalt with the cracks between individual sub-angular boulders filled with fossiliferous sedimentary rock. The exposure is capped by pillow basalt. At and near the bottom of the cracks is a black silty mudstone containing pulverized shell hash with many small to minute gastropods that are complete and well preserved. The silty mudstone is poorly indurated, and shells can be removed intact. The new species described in this paper were found in this silty mudstone, and the specimens, which could easily be missed by a cursory examination of the outcrop, are fragile and easily broken if care is not taken in their removal from the rock. Also in the silty mudstone are some scattered, large (up to 2.5 cm) fragments of colonial corals, gastropods, and bivalves. The abundance of shell hash is usually so great that it forms coquinas. Near the tops of the cracks, there are smaller, angular basalt clasts, up to 5 cm across, supported by white-to-gray muddy siltstone and sandstone with pulverized shell hash containing some scattered large (up to 3 cm) disarticulated bivalves and colonial-coral fragments. Locally, there are also patches of well-indurated, white-to-gray muddy siltstone with a great abundance of fragments of coralline algae.

The macrofauna at CSUN loc. 1563 is a mixture of rocky intertidal and shallow-subtidal taxa. There are many shells of the gastropods *Nerita* and *Arene* and the bivalve *Barbatia*. These taxa, plus *Emarginula*, *Haplocochlias*, and *Mitrella*, as well as the abundant fragments of colonial corals and coralline algae, indicate a warm-water, rocky intertidal environment. Modern *Nerita*, *Arene*, *Barbatia*, and *Mitrella* are indicative of rocky shores in tropical waters, and modern *Emarginula* live on rocky bottoms, intertidally to several hundred meters deep, usually in tropical waters (Keen, 1971; Abbott & Dance, 1982). Modern *Haplocochlias* live intertidally to 10 m on hard substrates in tropical waters (Keen, 1971; Hickman & McLean,

1990). The presence of the marine pulmonate *Ovatella* further confirms an intertidal, or even a supratidal environment. Modern species of *Ovatella* are air breathers that can tolerate short submersion at the highest spring tides and are never out of the reach of salt and spray in the following environments: high tidal or supratidal, upper shore of estuaries, or salt marshes and the fringes of salt marshes (Morton, 1955). Also at CSUN loc. 1563, there is a diverse assemblage of other mollusks that elsewhere on the Pacific coast of North America are indicative of shelflike depths where silty deposits accumulated. These mollusks include the gastropods *Turritella*, *Bittium*, *Pachycrommium*, *Colwellia*, and *Conus*, and the bivalves *Venericardia*, *Glyptoactis*, and *Corbula*.

The extrusion of the basalts in the vicinity of CSUN loc. 1563 caused shoaling and the establishment of a rocky shoreline community where *Nerita*, *Arene*, *Barbatia*, *Emarginula*, *Haplocochlias*, and *Mitrella* lived alongside colonial corals and coralline algae. The pounding surf broke and pulverized most of the larger macro-invertebrates, but many of the small to minute gastropods escaped destruction. All the shell material, as well as the muddy debris and clasts of basalt, were transported a short distance seaward where they were deposited in cracks between individual boulders of basalt. These boulders were adjacent to where mollusks like *Turritella* and *Venericardia* lived, and some of their shells also were washed into the cracks between the boulders. The minute-shelled *Lapsigyrus crescentensis* and *Linearia* (L.) *louellasaulae*, a tellinid, may have also lived among the *Turritella* and *Venericardia* because modern *Lapsigyrus* live in shallow water (approximately 20 m depth) in warm-water bays (Shasky, 1970; Keen, 1971), and modern tellinids are nearshore to offshore burrowers (Abbott & Dance, 1982). Continued extrusion of basalt covered this habitat before encrusting organisms could attach to the cobbles and boulders, and further protected the deposit from erosion.

The sedimentary rocks at CSUN loc. 1563 can be assigned to the "Capay Stage" (middle lower Eocene) on the basis of the presence of *Turritella andersoni* Dickerson, which is restricted to this stage elsewhere on the Pacific coast of North America (Squires & Demetron, 1992).

At the Rock Candy Mountain locality, a thin exposure of sedimentary rock is in a roadcut and in a small nearby quarry. The lithologies are the same as those at CSUN loc. 1563, except that there is less mudstone matrix, less coralline-algal remains, and more large bivalves. There are also fewer small to minute gastropods, and the only new species of gastropod present in the silty mudstones at CSUN loc. 1564 is *Emarginula washingtoniana*.

The environment of deposition and age of the sedimentary rocks at CSUN loc. 1564 are the same as for CSUN loc. 1563, on the basis of identical lithologies and similar fossil content. Globerman et al. (1982:1153) also reported a shallow-water depth (< 50 m) for the rocks at CSUN loc. 1564, on the basis of benthic foraminifera, and they

also reported an early Eocene age (K/Ar age of 53.1 ± 2 m.y.) for the associated basalts.

SYSTEMATIC PALEONTOLOGY

Class Gastropoda Cuvier, 1797

Subclass Prosobranchia Milne-Edwards, 1848

Order Vetigastropoda Salvini-Plawén, 1980

Family FISSURELLIDAE Fleming, 1822

Genus *Emarginula* Lamarck, 1801

Type species: *Emarginula conica* Lamarck, 1801, by original designation, Miocene through Recent, living in Finland and coasts of Great Britain to the Adriatic Sea (Palmer, 1937).

Emarginula washingtoniana
Squires & Goedert, sp. nov.

(Figures 2–5)

Diagnosis: A tall *Emarginula* with apex not strongly curved posteriorly, moderately deep slit, and 16 primary radial ribs.

Description: Shell small, high conical, up to 4 mm high, with height about two-thirds of length. Apex situated about one-third the distance from posterior end, curved posteriorly, with beaklike appearance. Anterior slope convex and steep; posterior slope concave. Anal slit situated at anterior margin, narrow and moderately deep, measuring 0.5 mm deep (=11 percent of shell length). Area of slit band coincident with raised area extending nearly to apical area. Sculpture of about 16 primary radial ribs originating near apex. Interspaces between primary radial ribs with a single, moderately strong, secondary radial rib; rarely a single tertiary radial rib in interspace between a primary and a secondary radial rib. Radial sculpture crossed by intermittently prominent growth rugae, especially near margin of aperture and on posterior slope. Aperture ovate-circular.

Dimensions of holotype: Length 4.5 mm, width 3 mm, height 3 mm.

Holotype: LACMIP 12279.

Type locality: CSUN loc. 1563, Larch Mountain area, Black Hills, southwestern Washington, 47°59'03"N, 123°8'12"W.

Paratype: LACMIP 12280.

Discussion: Five specimens of the new species were found. Except for the holotype, they are fragments. Four of the specimens are from CSUN loc. 1563, and one specimen is from CSUN loc. 1564. The holotype has been slightly crushed, and this crushing may have affected the area of the slit band, causing it to appear raised. The holotype

also has an encrusting polychaete worm shell attached to it near the apex (Figures 2–4).

The new species is similar to *Emarginula mariae* Cossmann (Cossmann & Pissarro, 1910–1913:pl. 2, fig. 9–4) from the upper Paleocene (Thanetian Stage) of the Paris Basin, France. *Emarginula washingtoniana* differs in the following features: shell taller, apex not as strongly curved posteriorly, and concentric ribbing not as well developed.

In the position of its apex, *E. washingtoniana* is more similar to European Cretaceous species than to Caribbean Cretaceous species. The European species usually have an apex that is situated well forward of the posterior margin, whereas the Caribbean species have an apex that distinctly overhangs the posterior margin (Sohl, 1992).

Cox & Keen (1960) reported the geologic range of *Emarginula* to be Jurassic to Recent. Haber (1932) listed 41 species from Jurassic rocks, and all are restricted to Europe. The species occur mainly in shallow-water carbonate-bank, or reef-associated assemblages (Sohl, 1992). Sohl (1992) listed 80 species from Cretaceous rocks, most restricted to Europe. They are most common in environments similar to their Jurassic occurrence. Only three Cretaceous species have been described from the Western Hemisphere (Sohl, 1992). Two are from the Caribbean region, and the third is *E. gabbi* Stewart (1926:313, pl. 23, fig. 10 [= a replacement name for *E. radiata* Gabb, 1864:140, pl. 21, figs. 102, 102a]) from Cretaceous strata in northern California. The new species differs from *E. gabbi* Stewart in the following features: aperture ovate-circular rather than elongate, steeper sides, posterior slope more concave, and fewer ribs (16 rather than 20).

The number of known early Tertiary species of *Emarginula* is far less than that known for the Mesozoic. Cossmann & Pissarro (1910–1913) illustrated only two Paleocene species and seven Eocene species of *Emarginula* from the Paris Basin, France. Similarly, Glibert (1962) listed two Paleocene, six Eocene, and one Oligocene species from rocks of Europe.

Palmer & Brann (1966) listed only one named species and two unnamed species (based on internal molds) of *Emarginula* from middle to upper Eocene rocks of the southeastern United States. The new species differs from these *Emarginula* by being much smaller and with a higher shell.

Since the Oligocene, *Emarginula* has been represented by a relatively low number of species. Today, the geographic range is mostly in warm waters in Europe, the Mediterranean, Georgia (U.S.A.) to Brazil, the Philippines, New Zealand, Chile, Galápagos Islands, Colombia, and the Gulf of California (McLean, 1970; Abbott & Dance, 1982).

Emarginula washingtoniana is the first Cenozoic species of this genus to be reported from the Pacific coast of North America. Other than the Cretaceous species *E. gabbi* Stewart, the genus was unknown in this area until the description of a Recent species from the Gulf of California (Shasky, 1961). Only three other species of Recent *Emarginula*

are known from the eastern Pacific: two from Chile and one from the Galápagos Islands and Colombia (McLean, 1970).

Etymology: The species is named for the state of Washington.

Occurrence: "Capay Stage" (middle lower Eocene). Crescent Formation, Larch Mountain and Rock Candy Mountain, Washington (CSUN locs. 1563, 1564).

Family TROCHIDAE Rafinesque, 1815

Genus *Calliovarica* Vokes, 1939

Type species: *Calliovarica eocensis* Vokes, 1939, by original designation, early Eocene, central California.

Calliovarica pacifica Squires & Goedert, sp. nov.

(Figures 6–8)

Diagnosis: Moderately low-spined *Calliovarica* having teeth on inner lip, denticles on outer lip, and narrow umbilicus.

Description: Shell moderately small, up to 12.5 mm in height, turbiniform, thick, with four to five convex whorls showing moderate rate of expansion. Spire moderately high, body whorl large, whorls subtabulate anterior to moderately impressed suture. Basal edge of body whorl angulate. Penultimate whorl with five to six prominent spiral ribs. Body whorl with approximately 14 spiral ribs; three to four at periphery strongest, eight ribs on base of body whorl approximately equal to two ribs nearest suture. All spiral ribs crossed by prosocline axial ornament producing reticulate (beaded to scaly) pattern. Outer shell layer generally missing; inner layer nacreous and showing spiral ribs but lacking axial ornament. Aperture slightly oblique, circular, outer lip reflected and strongly thickened with multiple (about 10) irregular denticles. Inner lip calloused with a prominent tooth and two smaller teeth anteriorly. Heavy rim of parietal callus continuous with inner and outer lips. Narrow umbilicus, nearly filled by columellar callosity.

Dimensions of holotype: Height 13.5 mm, width 12.5 mm.

Holotype: LACMIP 12281.

Type locality: CSUN loc. 1563, Larch Mountain, Washington, 47°59'03"N, 123°8'12"W.

Paratype: LACMIP 12282, CSUN loc. 1563.

Discussion: Eleven specimens were found, and all are from CSUN loc. 1563. Most of the shells are chalky due to weathering and/or diagenesis, and fall apart when collected. The holotype of the new species is a resting-stage individual on the basis of the well-developed apertural characteristics and the presence of the thickened outer lip (J. H. McLean, personal communication).

Previously, the genus *Calliovarica* was monotypic, represented by *C. eocensis* Vokes (1939:183, pl. 22, figs. 20, 23, 25, 28) known only from UCMP loc. 1817 in Urruttia Canyon, central California. Squires (1988) reported that this locality is in the "Capay Stage" Cerros Shale Member of the Lodo Formation. The new species differs from *C. eocensis* in the following features: shorter spire, presence of teeth on inner lip and denticles on outer lip, and narrowly umbilicate. The new species extends the geographic range of *Calliovarica* into Washington.

Hickman & McLean (1990) included *Calliovarica* within the chilodontine trochids, whose shell morphology is distinguished by apertural thickening and denticulation, a circular aperture produced by this apertural thickening, and reticulate or cancellate shell sculpture.

Etymology: The species is named for the Pacific Ocean.

Occurrence: "Capay Stage" (middle lower Eocene). Crescent Formation, Larch Mountain, Washington (CSUN loc. 1563).

Family SKENEIDAE Clark, 1851

Genus *Haplocochlias* Carpenter, 1864

Type species: *Haplocochlias cyclophoreus* Carpenter, 1864, by original designation, Recent, western Mexico.

Haplocochlias montis Squires & Goedert, sp. nov.

(Figures 9–11)

Diagnosis: A *Haplocochlias* with fine spiral ribbing, nearly closed umbilicus, and denticles on outer and inner lips.

Description: Shell minute, up to 2.5 mm in height, turbiniform, with three to four convex whorls, increasing rapidly in size. Spire low, body whorl globose with medial angulation. Suture distinct and impressed. Whorls with many closely spaced, fine spiral ribs, coarsening toward base of body whorl. Aperture ovate, nearly continuous, oblique. Outer lip slightly reflected, prosocline, many small denticles, especially on anterior end. Inner lip flattened anteriorly, with a low ridge near inner margin and paralleling it; ridge terminating posteriorly with a protuberance. Umbilicus nearly closed, slitlike.

Dimensions of holotype: Height 2.5 mm, width 2.5 mm.

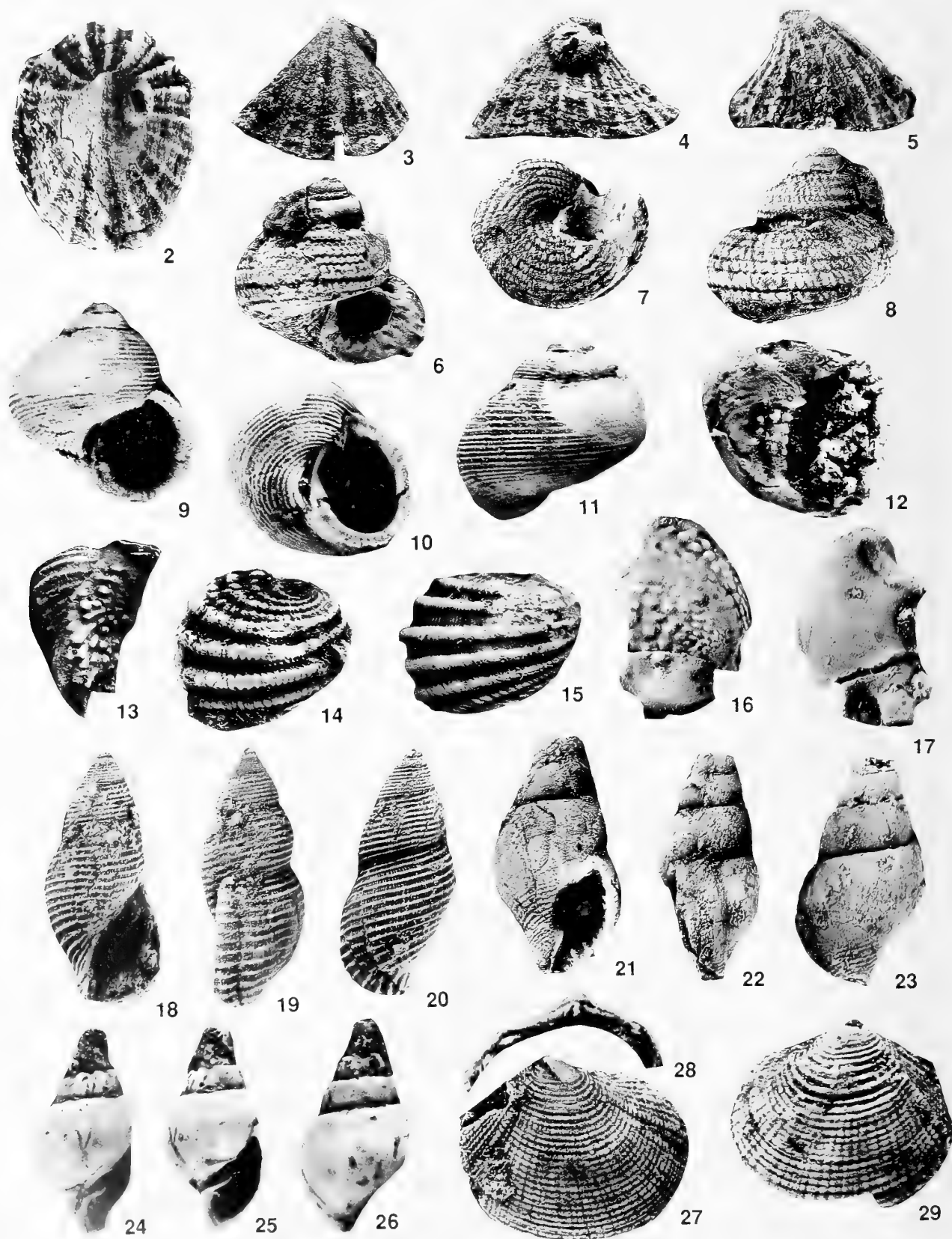
Holotype: LACMIP 12283.

Type locality: CSUN loc. 1563, Larch Mountain, Washington, 47°59'03"N, 123°8'12"W.

Paratype: LACMIP 12284.

Discussion: Six specimens were found, and all are from CSUN loc. 1563. The holotype is the largest specimen. Most of the others are fragments.

The new species resembles *H. cyclophoreus* Carpenter (1864; Keen, 1971:fig. 119; Hickman & McLean, 1990:fig. 95B), the type species of the genus, but differs in the



following features: thinner shell, stronger spiral ribbing, and an aperture with denticles.

Haplocochlias previously was known with certainty only as a Recent genus in the eastern Pacific and western Atlantic (Hickman & McLean, 1990). The fossil record of the family Skeneidae had been reported as early Miocene to Recent, with some of the Eocene species assigned to *Collonia* Gray, 1850 by Cossmann (1918:pl. 1, figs. 42–47; pl. 2, figs. 1–3) possibly included in the family (Hickman & McLean, 1990). The new species has a much higher spire and a much narrower umbilicus than these Eocene species, which are from the Paris Basin, France.

Cossmann & Pissarro (1910–1913:pl. 4, figs. 33–1 to 33–4, 33–7 to 33–13; pl. 5, figs. 33–14 to 33–28) illustrated additional Eocene species of *Collonia* from the Paris Basin, France. Of these, the new species is most like *Collonia* (*Cirsochilus*) *grignonensis* (Deshayes, 1864–1866:pl. 60, figs. 22–24 [= *Turbo grignonensis*]; Cossmann & Pissarro, 1910–1913:pl. 4, fig. 33–13) from middle Eocene (Lutetian Stage) strata. The new species differs in the following features: finer spiral ribbing on body whorl angulation, an aperture with denticles, and no beaded umbilical cord.

The new species is the first positively known fossil species of *Haplocochlias* and the earliest known representative of family Skeneidae.

Etymology: The species name is from the Latin *montis*, mountain, and refers to the position of the type locality of this species.

Occurrence: “Capay Stage” (middle lower Eocene). Crescent Formation, Larch Mountain, Washington (CSUN loc. 1563).

Order Neritoida Golikov & Starobogatov, 1975

Family NERITIDAE Rafinesque, 1815

Genus *Nerita* Linné, 1758

Type species: *Nerita peloronta* Linné, 1758, by subsequent designation (Montfort, 1810), Recent, Caribbean Sea.

Subgenus *Theliostyla* Mörch, 1852

Type species: *Nerita albicilla* Linné, 1758, by subsequent designation (Kobelt, 1879), Recent, Indo-Pacific.

Nerita (*Theliostyla*) *olympia* Squires & Goedert, sp. nov.

(Figures 12–17)

Diagnosis: A *Theliostyla* with a body whorl having seven to eight noded carinae separated by interspaces as wide as the carinae.

Description: Shell small, up to 7 mm in height, broader than high, with rapidly expanding body whorl. Spire flattened, apex barely elevated above nearly flat dorsal surface. Dorsal surface with three to four noded spiral ribs (excluding carina on shoulder) that become coarser and more elevated toward outer lip. Body whorl with seven to eight, evenly spaced and usually equal-strength nodose carinae becoming, in some specimens, increasingly coarse toward base of body whorl. Interspaces approximately as wide as carinae and with or without a single, beaded spiral rib. Axial riblets fine, crossing spiral carinae and interspaces. Aperture large, quadrate. Outer lip flared, grooved at body-

Explanation of Figures 2 to 29

All specimens coated with ammonium chloride. Pictures taken by the senior author. All from CSUN loc. 1563.

Figures 2–5. *Emarginula washingtoniana* Squires & Goedert, sp. nov., holotype LACMIP 12279. Figure 2. Dorsal view, ×9.2. Figure 3. Anterior view, ×10. Figure 4. Left-lateral view, ×8.7. Figure 5. Right-lateral view, ×7.6. Figures 6–8. *Callovarica pacifica* Squires & Goedert, sp. nov., holotype LACMIP 12281. Figure 6. Apertural view, ×2.4. Figure 7. Umbilical view, ×2.5. Figure 8. Abapertural view, ×2.8. Figures 9–11. *Haplocochlias montis* Squires & Goedert, sp. nov., holotype LACMIP 12283. Figure 9. Apertural view, ×14.4. Figure 10. Umbilical view, ×13. Figure 11. Abapertural view, ×13. Figures 12–17. *Nerita* (*Theliostyla*) *olympia* Squires & Goedert, sp. nov. Figure 12. Holotype LACMIP 12285, apertural view, ×16. Figure 13. Paratype LACMIP 12286, deck area, ×9.5. Figure 14. Paratype LACMIP 12287, abapertural view, ×4.6. Figure 15. Holotype LACMIP 12285, abapertural view, ×11. Figures 16–17. Para-

type LACMIP 12288, operculum, ×11. 16. Exterior view. 17. Interior view. Figures 18–20. *Lapsigyrus crescentensis* Squires & Goedert, sp. nov., holotype LACMIP 12289, ×8. Figure 18. Apertural view. Figure 19. Lateral view showing outer lip. Figure 20. Abapertural view. Figures 21–23. *Mitrella* (*Mitrella*) *blackhillsensis* Squires & Goedert, sp. nov., holotype LACMIP 12291. Figure 21. Apertural view, ×7.8. Figure 22. Lateral view showing outer lip, ×7.5. Figure 23. Abapertural view, ×7.5. Figures 24–26. *Ovatella* (*Myosotella*) *coneyi* Squires & Goedert, sp. nov., holotype LACMIP 12292, ×14. Figure 24. Apertural view. Figure 25. Apertural view, rotated so as to reveal parietal plica. Figure 26. Abapertural view. Figures 27–29. *Linearia* (*Linearia*) *louellasaulae* Squires & Goedert, sp. nov. Figure 27. Holotype LACMIP 12294, right valve, ×10.3. Figure 28. Paratype LACMIP 12295, right-valve hinge, ×14.6. Figure 29. Paratype LACMIP 12296, left valve, ×12.3.

whorl carinae. Inner lip with seven teeth. Two posterior-most teeth stronger than rest, with tooth next to posterior-most tooth strongest. Five small, subequal teeth medially. Deck with numerous small tubercles, round to elongate, arranged loosely in rows. Operculum calcareous with peg-like projection anteriorly and two small protuberances on inner lip side; exteriorly with numerous small tubercles medially and posteriorly arranged loosely in rows; interiorly smooth.

Dimensions of holotype: Height 2 mm, width 3 mm.

Holotype: LACMIP 12285.

Type locality: CSUN loc. 1563, Larch Mountain, Washington, 47°59'03"N, 123°8'12"W.

Paratypes: LACMIP 12286 to 12288, all from CSUN loc. 1563.

Discussion: Thirty specimens of *Nerita olympia* were found, and all are from CSUN loc. 1563. Most of the shells are chalky due to weathering and/or diagenesis and fall apart when removed from the brittle, silty mudstone that encloses them. Ten specimens of the operculum were found, and they are also all from CSUN loc. 1563.

The new species is similar to *Nerita* (*T.*) *héberti* Szöts (1953:30, 141–142, pl. 2, figs. 3–5) from the Eocene of Hungary. The new species differs by having fewer carinae on the dorsal surface and on the body whorl and stronger carinae on the body whorl. Szöts (1953) did not assign his species to the subgenus *Theliostyla*, but *N. héberti* has a dentate outer lip, a granulate deck area, and a finely dentate inner lip. These features are listed by Keen & Cox (1960) as being diagnostic of *Theliostyla*, hence Szöts' species belongs in *Theliostyla*.

There are only two other known species of *Nerita* (*Theliostyla*) from the Pacific coast of North America. One is *N. (T.) triangulata* Gabb (1869:170, pl. 28, figs. 52, 52a) from middle lower Eocene ("Capay Stage") to upper Eocene ("Tejon Stage") deposits from southern California to southwestern Oregon. Squires (1992b) reviewed the considerable range of morphologic variation of this species. The new species differs by having more carinae on the body whorl, more widely spaced carinae, and fewer or no ribs in the interspaces. The other known species is *N. (T.)* n. sp. (?) Woods & Saul (1986:649, figs. 6.13, 6.16, 6.17) from the upper Paleocene? or lower Eocene? ("Capay Stage") Sepultura Formation, Baja California Sur, Mexico. The new species differs by having many fewer carinae on the body whorl and more widely spaced carinae.

There are three known species of *Nerita* s.l. from Eocene rocks along the Pacific coast of North America. Two, *N. washingtoniana* Weaver & Palmer (1922:28–29, pl. 11, fig. 4) from the upper middle Eocene Cowlitz Formation, southwest Washington, and *N. vokesi* Durham (1944:156, pl. 17, figs. 11, 12) from the upper Eocene of northwest Washington (Squires, 1992b), are quite different from the new species because they possess smooth body whorls. The

third, *N. cowlitzensis* Dickerson (1915:58–59, pl. 5, fig. 7a, b) from the Cowlitz Formation in southwest Washington also differs significantly from the new species by possessing a body whorl with only minute sculpture.

Theliostyla probably originated in the Old World Tethyan paleobiotic province and immigrated to the Pacific coast of North America during the early Eocene (Squires, 1992b).

Etymology: The species is named for the city of Olympia, Washington, which is near the type locality of the new species.

Occurrence: "Capay Stage" (middle lower Eocene). Crescent Formation, Larch Mountain, Washington (CSUN loc. 1563).

Order Caenogastropoda Cox, 1960

Family RISSOIDAE Gray, 1847

Genus *Lapsigyrus* Berry, 1958

Type species: *Alvania contrerasi* Jordan, 1936 (= *Alaba mutans* Carpenter, 1857), by original designation, Pleistocene to Recent, west Mexico.

Lapsigyrus crescentensis Squires & Goedert, sp. nov.

(Figures 18–20)

Diagnosis: A *Lapsigyrus* having an elongate shell with 16 to 17 spiral threads on the body whorl.

Description: Shell minute, up to 5.5 mm in height, elongate, ovately conic, having approximately six convex whorls; spire high. Nucleus of 2½ whorls, smooth and conical. Spiral sculpture of thin ribs with 10 to 11 on penultimate whorl and 16 to 17 on body whorl; five terminal ribs on base are about twice as strong as preceding ribs; channels between spiral ribs filled with innumerable minute axial threads producing finely netted appearance within channels only. Suture indistinct. Body whorl strongly descending, exposing anteriormost part of preceding whorl. Aperture large, D-shaped. Outer lip slightly opisthocline, with narrow varix.

Dimensions of holotype: Height 5.5 mm, width 2.3 mm.

Holotype: LACMIP 12289.

Type locality: CSUN loc. 1563, Larch Mountain, Washington, 47°59'03"N, 123°8'12"W.

Paratype: LACMIP 12290, CSUN loc. 1563.

Discussion: Three specimens were found, and they are all from CSUN loc. 1563. The holotype is the largest specimen. The new species is remarkably similar to the living *Lapsigyrus myrioshirissa* Shasky (1970:189, fig. 3) from west Mexico. The new species differs by having a more elongate shell with thicker and more widely spaced spiral ribs.

Previously, the geologic range of genus *Lapsigyrus* was Pleistocene to Recent, with a single Pleistocene species and a few living species (Shasky, 1970; Keen, 1971). The geographic range of the genus was from Magdalena Bay, Baja California Sur, Mexico, to Costa Rica (Keen, 1971; Ponder, 1985). The new species extends the geologic range to the early Eocene and the geographic range to Washington.

Etymology: The species is named for the Crescent Formation.

Occurrence: "Capay Stage" (middle lower Eocene). Crescent Formation, Larch Mountain, Washington (CSUN loc. 1563).

Family COLUMBELLIDAE Swainson, 1840

Genus *Mitrella* Risso, 1826

Type species: *Mitrella flaminea* Risso, 1826, by subsequent designation (Cox, 1927), Recent, Mediterranean Sea.

Subgenus *Mitrella* s.s.

Mitrella (*Mitrella*) ***blackhillsensis***

Squires & Goedert, sp. nov.

(Figures 21–23)

Diagnosis: A small *Mitrella* having a broad body whorl and no teeth on inner lip.

Description: Shell small, up to 5.5 mm in height, oval-fusiform. Suture distinct and impressed. Spire high with flat-sided, smooth whorls. Body whorl somewhat broad, smooth. Neck and siphonal fasciole areas with many fine spiral ribs. Aperture ovate. Outer lip varicose with 13 denticles on interior. Inner lip smooth. Anterior notch narrow.

Dimensions of holotype: Height 5.5 mm (incomplete); width 3 mm.

Holotype: LACMIP 12291.

Type locality: CSUN loc. 1563, Larch Mountain, Washington, 47°59'03"N, 123°8'12"W.

Discussion: Only two specimens were found. The new species is most similar to *Mitrella richthofeni* (Gabb, 1869: 10, pl. 2, fig. 16) from Pliocene beds in northern California (Keen & Benton, 1944) and tentatively from lower Miocene beds in southern California (Loel & Corey, 1932). The new species differs in the following features: smaller size, broader body whorl, and no teeth on inner lip.

Wenz (1941) reported the geologic range of *Mitrella* s.s. to be Miocene to Recent. Several late Cenozoic species are known from the Pacific coast of North America. *Mitrella tenuilineata* (Clark, 1918:173, pl. 22, figs. 2, 3) has been reported from Oligocene beds in northern California, but

does not belong to *Mitrella* s.s. because it has spiral ribbing over the entire teleoconch.

The new species is the earliest record of *Mitrella* s.s.

Etymology: The species is named for the Black Hills, Washington.

Occurrence: "Capay Stage" (middle lower Eocene). Crescent Formation, Larch Mountain, Washington (CSUN loc. 1563).

Subclass Pulmonata Milne-Edwards, 1848

Order Basommatophora Schmidt, 1855

Family ELLOBIIDAE H. & A. Adams, 1855

Genus *Ovatella* Bivona, 1832

Type species: *Ovatella punctata* Bivona, 1832 [= *Auricula firminii* (Payraudeau, 1826)], by original designation, Recent, Mediterranean Sea.

Subgenus *Myosotella* Monterosato, 1906

Type species: *Auricula myosotis* Draparnaud, 1801, by original designation, Recent, Europe and both east and west coasts of the United States.

Ovatella (*Myosotella*) ***coneyi***

Squires & Goedert, sp. nov.

(Figures 24–26)

Diagnosis: A narrow shelled *Ovatella* having subtabulate whorls, inner lip with two plicae, and anterior end of aperture pointed.

Description: Shell minute, up to about 3 mm in height, narrowly ovate-fusiform, with approximately five convex whorls; spire elevated (approximately 36 percent of shell height). Suture distinct and impressed. Whorls smooth and subtabulate near suture; middle of body whorl with very faint shoulder. Aperture ovate, anterior end pointed and flattened. Inner lip with two plicae continuing deep inside of aperture, anteriormost plica formed by turning of lip within the aperture and twice as strong as the posteriormost plica; posteriormost plica in parietal area. Outer lip broken off.

Dimensions of holotype: Height 2.75 mm, width 1.5 mm.

Holotype: LACMIP 12292.

Type locality: CSUN loc. 1563, Larch Mountain, Washington, 47°59'03"N, 123°8'12"W.

Paratype: LACMIP 12293, CSUN loc. 1563.

Discussion: Only two specimens were found and both are from CSUN loc. 1563. The new species resembles some variants of the living species *O. (M.) myosotis* (Draparnaud, 1801), a Mediterranean and eastern Atlantic species

dispersed by man to the east and west coasts of North America, the West Indies, South Africa, Australasia, and New Zealand (Climo, 1982). *Ovatella* (*M.*) *myosotis* shows considerable variation in the number of teeth on the inner and outer lips. The inner lip can have two to four teeth, and the outer lip can have one tooth or none (Climo, 1982). The new species resembles those specimens of *O. (M.) myosotis* that have two teeth on the inner lip and are without teeth on the outer lip (e.g., Climo, 1982:fig. 1A; and a few specimens in LACM lot 46780 from Purfleet, Essex, England). When compared to these particular examples, the new species differs in the following features: smaller size, spire whorls less convex, suture more impressed, subtabulate rather than non-tabulate whorls, base of body whorl more constricted, and aperture more elongate anteriorly.

Climo (1982) discussed the nomenclatural history of the family name that *Ovatella* should be assigned to, and Paulson (1957) reviewed the complex history of the genus name *Ovatella*. Zilch (1959–1960) discussed synonyms.

Zilch (1959–1960) reported the geologic range of *Ovatella* to be Paleocene to Recent. The early Tertiary species are from the Paris Basin, France, and the new species somewhat resembles *Ovatella (Myosotella) depressa* (De-shayes, 1864–1866:pl. 58, figs. 19–21; Cossmann & Pissarro, 1910–1913:pl. 58, fig. 256–8) from lower Eocene (Cuisian Stage) strata of the Paris Basin. The new species differs in the following features: smaller size, body whorl much less inflated near the suture, no spiral band anterior to suture, anterior end of aperture more pointed, no parietal callus, and no tendency to have more than one parietal plica.

Ovatella (Myosotella) coneyi is the first record of a marine pulmonate in the lower Tertiary of the Pacific coast of North America.

Etymology: The new species is named in memory of Charles Clifton Coney, who made valuable contributions to the study of Recent freshwater bivalves and terrestrial pulmonates.

Occurrence: "Capay Stage" (middle lower Eocene). Crescent Formation, Larch Mountain, Washington (CSUN loc. 1563).

Class Bivalvia Linné, 1758

Order Veneroida H. & A. Adams, 1856

Family TELLINIDAE de Blainville, 1814

Genus *Linearia* Conrad, 1860

Type species: *Linearia metastrata* Conrad, 1860, by monotypy, Late Cretaceous, Alabama.

Subgenus *Linearia* s.s.

Linearia (Linearia) louellasaulae
Squires & Goedert, sp. nov.

(Figures 27–29)

Diagnosis: A minute, circular-ovate *Linearia* having beaks located posteriorly, radial ribbing weak on center of valves, and posterior slope with different curvature than rest of valve.

Description: Valves minute, up to 3 mm high, thin and fragile, circular-ovate in plan: beaks small, slightly anterior of center; anterior end rounded, posterior end truncate. Sculpture of closely spaced, thin concentric ribs crossed by numerous fine radial ribs, except on umbonal area. Radial ribbing weak on center of valves. Intersections of concentric and radial ribs beaded, strongest anteriorly and posteriorly. Posterodorsal slope with different curvature than rest of valve and with approximately seven serrated ribs; rib on umbonal ridge coarsest. Right-valve hinge with two cardinals separated from each other by deep and narrow socket, anterior cardinal slender and obliquely directed downward; posterior cardinal shorter, thicker, and directed nearly vertically downward. Dorsal margin of right valve beveled to serve as laterals. Left-valve hinge not observable.

Dimensions of holotype: Height 3 mm, length 4 mm.

Holotype: LACMIP 12294.

Type locality: CSUN loc. 1563, Larch Mountain, Washington, 47°59'03"N, 123°8'12"W.

Paratypes: LACMIP 12295, 12296, both from CSUN loc. 1563.

Discussion: Eight specimens were found. Four are right valves, two are left valves, and two are fragments. The very delicate left valves are embedded in well-indurated matrix, and the hinges could not be exposed.

The new species is remarkably similar to *L. (L.) metastrata* Conrad (1860:279, pl. 46, fig. 7; Stephenson, 1923:329, pl. 84, figs. 1–5; Afshar, 1969:58, pl. 24, figs. 12–15; Keen, 1969, figs. E109–11a, 11b) from Upper Cretaceous strata of New Jersey, Maryland, North Carolina, Tennessee, and Mississippi. The new species differs in the following features: much smaller size, less elongate shell, beaks posteriorly located, posterior slope with a different curvature than rest of valve, and right-valve posterior cardinal thicker and not oblique.

Keen (1969) reported that the geologic range of *Linearia* s.s. is Early through Late Cretaceous, with species in Europe, North America, and Africa, but Stoliczka (1871:pl. 5, figs. 6, 7) reported *Linearia* from the Cretaceous of southern India. The North American species are primarily from the Upper Cretaceous of the east coast of the United States from New Jersey to Texas (Stephenson, 1923, 1941; Wade, 1926).

Only a few species of *Linearia* are known from the Pacific coast of North America. *Linearia suciensis* Whittes (1879:146–147, pl. 17, fig. 12) has the external features of *Linearia*, but the hinge characters are unknown and the only known specimen has been lost. This species

was found in Cretaceous rocks of Sucia Island in the Strait of Georgia, northwest Washington. These rocks are the Cedar District Formation, and the highest fossiliferous beds on the island have ammonites indicative of middle Campanian age (L. R. Saul, personal communication). The new species differs from *L. suciensis* in the following features: beaks more posteriorly located, posterior more truncate, radial ribs on ventral margin, coarser radial ribs on dorsal areas, and a distinct postero-dorsal umbonal ridge.

Whiteaves (1903:377) placed *L. suciensis* in synonymy with *Asaphis multicosata* Gabb (1869:181, pl. 29, fig. 70) from Crooked Creek, central Oregon. The type locality of *A. multicosata* is somewhat vague. There are Cenomanian strata along the Crooked River (Jones, 1960:438), however, and Gabb's (1869:181) associated fossils suggest Gabb's material is from the same horizon as *A. multicosata*. Stewart (1930:284–285, pl. 4, figs. 8,9) also considered *L. suciensis* and *A. multicosata* to be the same and called them *Linearia multicosata* (Gabb). These two taxa are morphologically quite different, and it seems likely that they are not the same species. *Asaphis multicosata* lacks the fine, crowded concentric striae of *L. suciensis*, and *A. multicosata* is geologically older than *L. suciensis*.

Whiteaves (1879:147) assigned *Tellina meekiana* Whiteaves (1874:268, unnumbered plate, fig. 6) to *Linearia* (*Leiothyris*) *meekiana* (Whiteaves). This species was found in Cretaceous rocks of Gabriola Island, just west of Vancouver, British Columbia, Canada. Examination of the LACMIP-collection plaster cast of the holotype of *Tellina meekiana* revealed that this species is quite unlike a *Linearia*. Saul (1993) studied Cretaceous venerids from the Pacific coast of North America, and she put *T. meekiana* in synonymy with *Paraesa* (?) *lens* (Gabb, 1864:23, fig. 143). She also reported that *P. (?) lens* [= *Flaventia lens* (Gabb, 1864)] is a common species in deposits of Campanian age from southern British Columbia to southern California.

Dailey & Popenoe (1966) described the tellinid *Palaeomoera dyskritos* Dailey & Popenoe (1966:18–19, pl. 5, figs. 1, 2, 5) from the Upper Cretaceous Jalama Formation, Santa Barbara County, southern California. They mentioned that they thought that this species belonged to *Linearia* until they found a specimen that showed the hinge of the left valve. It contained only one oblique cardinal; hence, it could not be assigned to *Linearia*.

The new species is the youngest record of genus *Linearia* anywhere in the world.

Etymology: The species is named for LouElla Saul, in recognition of her many valuable contributions to the study of Cretaceous mollusks from the Pacific coast of North America.

Occurrence: "Capay Stage" (middle lower Eocene). Crescent Formation, Larch Mountain, Washington (CSUN loc. 1563).

ACKNOWLEDGMENTS

Gail H. Goedert helped collect the fossils. James H. McLean (LACM) gave much help in the identification of the gastropods and provided literature. LouElla R. Saul (LACMIP) gave much help in the identification of the bivalve and allowed access to her library. Edward C. Wilson (LACMIP) provided access to fossil collections and gave catalog numbers. Lindsey T. Groves (LACM) provided access to Recent collections and helped in obtaining literature. The manuscript benefited from reviews by Ellen J. Moore (Corvallis, Oregon) and LouElla R. Saul.

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CSUN 1563. At elevation of 2230 feet (680 m), exposed in roadcut on NE side of logging road, latitude 47°59'03"N, longitude 123°8'12"W, 300 m N and 50 m E of SW corner of section 1, T17N, R4W, and 500 m S32°E of Larch Mountain, Capitol Peak U.S. Geological Survey quadrangle, 7.5-minute, provisional edition 1986, Thurston County, Washington. Crescent Formation. Age: Middle early Eocene ("Capay Stage"). Collectors: J. L. & G. H. Goedert, July, 1992.

CSUN 1564. At elevation of 1738 feet (530 m), on N side of logging road, 800 m N and 50 m W of SE corner of section 25, T18N, R3W, and 950 m N25°W of Rock Candy Mountain, Summit Lake U.S. Geological Survey quadrangle, 7.5-minute, 1981, Thurston County, Washington. Crescent Formation. Age: Middle early Eocene ("Capay Stage"). Collectors: J. L. & G. H. Goedert, August, 1992.

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Observations on the Biology of *Maoricolpus roseus*
(Quoy & Gaimard) (Prosobranchia: Turritellidae)
from New Zealand and Tasmania

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Abstract. *Maoricolpus roseus* lives in high to moderate abundances in New Zealand, where it appears to prefer areas of coarse or at least firm substrates, moderate to strong currents, depths of 1-130 m and temperatures of 8-20°C. Its abundance in New Zealand seems to be positively correlated with availability of suspended food, negatively correlated with suspended terrigenous sediment, and not strongly correlated with degree of coastal upwelling. Substrate firmness may also be important in controlling its distribution and/or abundance. Some individuals have been observed alive in an unusual vertical orientation in crevices in rocks, but the significance of this orientation is unclear. Following its introduction into Tasmania by unknown means early in this century, *M. roseus* has increased dramatically in abundance, probably due to a lack of appropriate predators. In New Zealand, it is preyed upon by teleosts and starfish, whereas in Tasmania, mortality appears to be due mostly to storms. The oxygen isotopic profiles of *M. roseus* shells reflect seasonal temperature changes during the life of the animal. Comparison with a previous study on *Turritella gonostoma* from the Gulf of California suggests that *M. roseus* grows more slowly.

INTRODUCTION

This is the second in a series of papers documenting the natural history of Recent species of the family Turritellidae (see Allmon et al., 1992). These gastropods are diverse and abundant components of many fossil and living marine benthic communities; yet little is known about the biology of individual species (Allmon, 1988). Here we present new information and review the scattered literature on a single living species, *Maoricolpus roseus* (Quoy & Gaimard, 1834) from South Island, New Zealand, where it is native, and Tasmania, where it apparently has been introduced, and put this information into the wider context of what is known about other turritellid species, fossil and Recent. The results reported here reinforce the conclusions that turritellid ecology is heterogenous (Allmon, 1988), and that different environmental variables may control distribution and abundance in different species and locations (Allmon, 1992; Allmon & Dockery, 1992; Allmon & Knight, 1993). Voucher specimens have been deposited in the Florida Museum of Natural History and the Paleontological Research Institution.

GEOGRAPHIC DISTRIBUTION AND ENVIRONMENT

New Zealand

Until this century, *Maoricolpus roseus* was probably endemic to New Zealand and its immediately adjacent islands. It has long been reported to occur in very large numbers in Auckland and Manukau Harbours and Rangitoto Channel on North Island (Powell, 1937, 1979; Morton & Miller, 1968; Grange, 1979) and in high to moderate abundance in Otago Harbour on South Island (Ralph & Yaldwyn, 1956; up to 2440/m², fide Rainer, 1981) (Figure 1a). Powell (1937:374) stated that "in the main channel of the inner and upper sections of the Auckland Harbour," *M. roseus* "is so super-abundant that the dredge contents at a glance appear to be made up of this and very little else" (see also Morton & Miller, 1968:580–581). Grange (1979) noted that, although *M. roseus* is the most abundant mollusk in Manukau Harbour, it is subdominant to other macrobenthic species (e.g., crabs, polychaetes, ascidians). Grace (1972) described an "*Atrina-Paphirus-Maoricolpus* community" from subtidal channels of Whangateau Harbour near Auckland. Brook et al. (1981) described a "*Corallina-Maoricolpus-Notomithrax* association" in gravelly sediments at 1–7 m depth from another harbor on the east coast of North Island.

The species occurs elsewhere in New Zealand in lesser numbers (Figure 1a): in the Chatham Islands east of South Island ("from low water to 50 fathoms"; Powell, 1979: 125); in Tasman Bay, on the northern end of South Island ("in several fathoms"; Powell, *ibid*); offshore from the Otago Peninsula on the southeast coast of South Island (50–76 m depth; Probert & Wilson, 1984); in Fiordland on the southwest coast of South Island (Doubtful Sound;

alive to approximately 25 m depth, most abundant at about 16 m, empty shells to at least 37 m; R. Aiello, personal observation); and on Stewart Island (Paterson Inlet, Ulva Island; to about 16 m depth, most common at 4–8 m; R. Aiello, personal observation).

Powell (1937, 1979) believed that although *M. roseus* was occasionally found in sands, silts, and muds, it occurred most commonly and abundantly on shell gravel substrates. McKnight (1969) suggested that most or all of these coarse-substrate occurrences were tidal scour or lag deposits and not representative of normal habitat preferences of *M. roseus*. Powell (1950) designated *M. roseus* as a "secondary species" in his *Chlamys delicatula-Fusitriton* community," which he described as occurring along the Otago shelf on a "hard-sand, shelly or gravel bottom under the influence of strong, tidal currents" at depths of about 90–130 m. Benthic community studies by Probert et al. (1979) and Probert & Wilson (1984) showed that *M. roseus* was most abundant on the mid-shelf gravelly sediments off the eastern coast of South Island. Rainer (1981:29) noted that *M. roseus* "is found in a variety of environments, particularly where there is a firm sediment with at least moderate current speeds and with a variety of other species."

Fleming (1952) recorded *M. roseus* as dead shells from Foveaux Strait, an area also characterized by strong tidal currents and coarse sediments, and it seems to be apparent in underwater photographs of a similar current-swept ophiuroid-dominated community in Cook Strait (Hurley, 1959). These are perhaps similar to the "brachiopod-*Chlamys* community" described from a number of locations around New Zealand on coarse sediments subjected to currents (Fleming, 1950; Dell, 1951; Hurley, 1964; Estcourt, 1967). Dell (1951), for example, describes this community from Queen Charlotte Sound (northern South Island), where *M. roseus* is a common constituent, although known only as a dead shell. Dead *Maoricolpus* shells were also a major component of the samples reported by Estcourt (1967) from the outer Marlborough Sounds. Such assemblages are also well known in the New Zealand and Australian Tertiary (e.g., Chapman, 1914; Allan, 1937).

Our own observations indicate that at Portobello in Otago Harbour, *M. roseus* lives in or on very coarse pebble-and-shell gravels in the intertidal and shallow subtidal zone; in Doubtful Sound, it lives in crevices between boulders as well as in coarse pebble-and-shell gravels as well as in muddy sand; and in Paterson Inlet, Stewart Island, where it also occurs in coarse pebble-and-shell gravel (see also Willan, 1981) (Figure 2).

Maoricolpus roseus also occurs on or in finer sediments. McKnight (1969) includes *M. roseus* as a characterizing species in two similar assemblages: his "*Amphiura rosea-Dosinia lambata* community" occurring at depths of 1–50 m on sandy mud or mud and in his "*Nemocardium pulchellum-Dosinia lambata* community" occurring mainly at 18–50 m on muddy sand to mud. Fleming (1950) gives some information about the distribution of mollusks in the fjords of southern New Zealand and mentions that *M.*

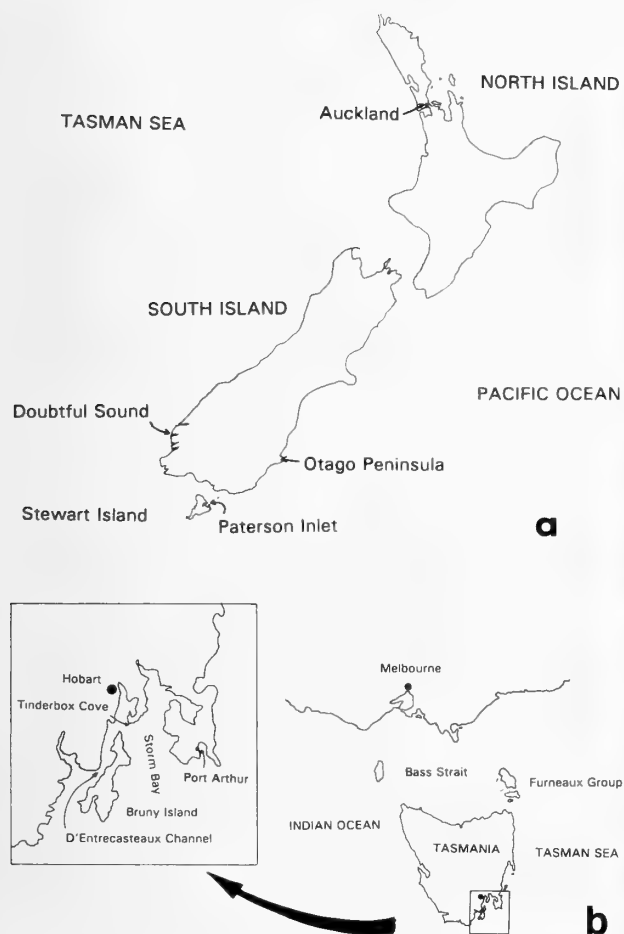


Figure 1

Maps of a. New Zealand, b. Tasmania, showing localities mentioned in text.

roseus was dominant at some stations (NGH 34, 41, 53) in Dusky Sound and Chalky Inlet that had a sandy mud or muddy sand substratum. Batham (1969) reported *M. roseus* to be abundant at sandy mud and mud stations in Glory Cove, at the entrance to Paterson Inlet. According to Batham, most of the cove bottom was dominated by the green alga *Lenormandia*. In Paterson Inlet, Willan (1981) found *M. roseus* commonly at most stations, and remarks in particular on its occurrence on a variety of sediment types. Similarly Hare (1992) indicates that *M. roseus* is a common species of the *Lenormandia* meadows of Paterson Inlet; these meadows probably play an important role in stabilizing the muddy bottoms. Thus, while *M. roseus* can be found on muddy bottoms, it may be excluded from the more unstable muddy bottoms where there is likely to be much resuspension of fines at the sediment-water interface.

M. roseus appears to have a relatively wide temperature tolerance in New Zealand. Oceanographically, New Zealand lies between colder, lower salinity subantarctic waters

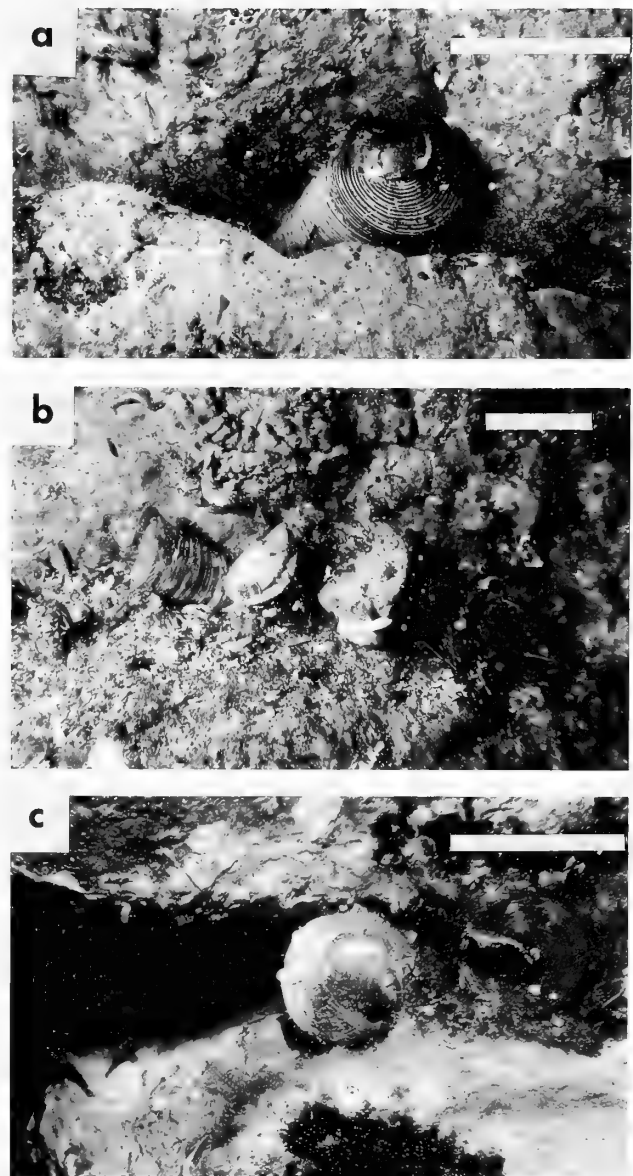


Figure 2

a-c. Living individuals of *Maoricolpus roseus* oriented vertically in cracks between boulders in Doubtful Sound, Fiordland, southwestern New Zealand. Depth approximately 20 m. Photos taken 10 February 1990. Scale bars = 2 cm.

to the southeast and warmer, higher salinity subtropical waters to the northwest (Vincent et al., 1991). Nearshore temperatures along the northwest coast of South Island are therefore usually higher than those along the southeast coast. Coastal upwelling occurs along the northwest coast (Probert & Anderson, 1986; Grieg et al., 1988; Vincent et al., 1991), but only episodically, and it is not comparable to the upwelling systems associated with eastern boundary currents elsewhere in the world. This is supported by studies of sediment geochemistry (Stoffers et al., 1984).

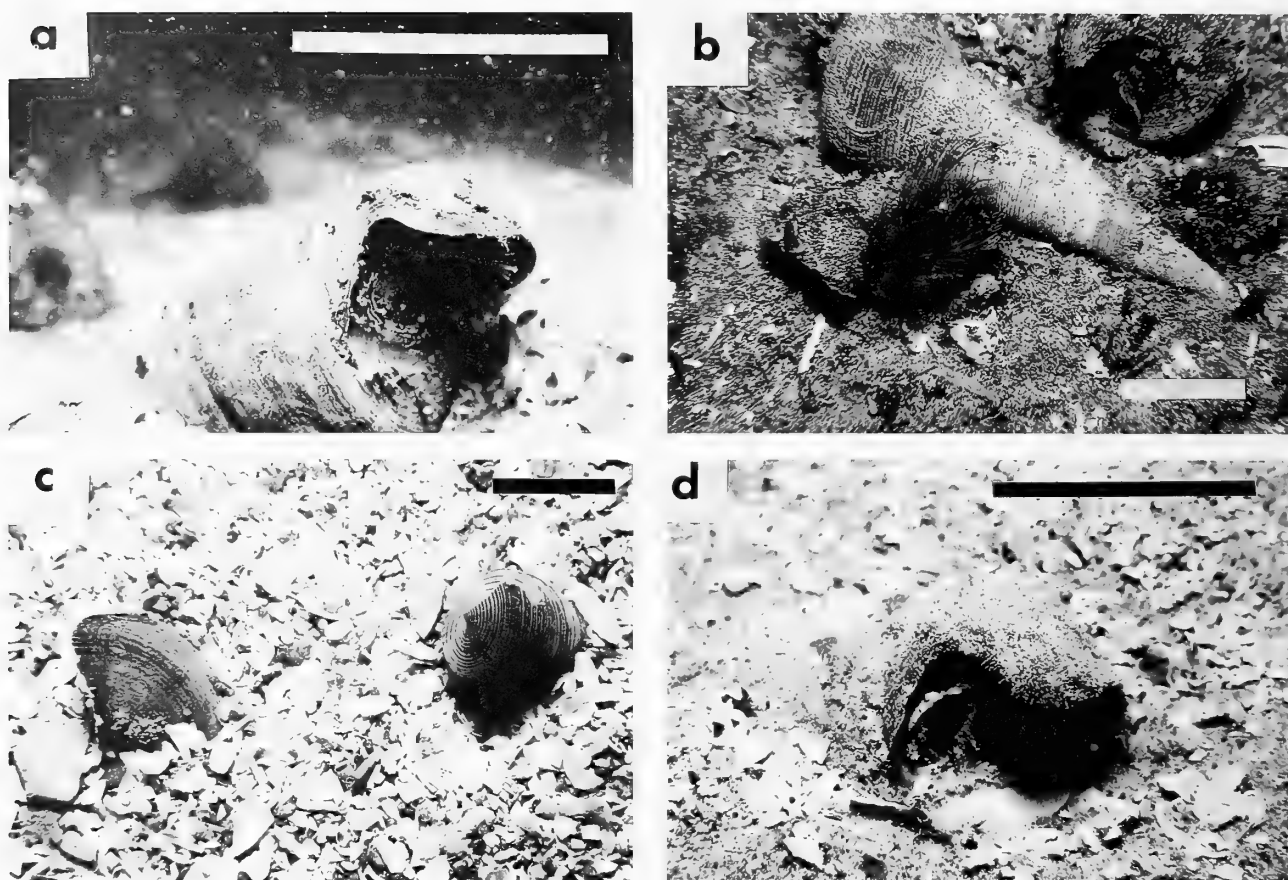


Figure 3

Living individuals of *Maoricolpus roseus* in situ in coarse sediments off southeastern Tasmania. a, b, d. Tinderbox Cove, at entrance to D'Entrecasteaux Channel; depth approximately 3 m. c. Frying Pan Point, Port Arthur. Depth 8–10 m. Photos taken 25–30 July 1991. Scale bars = 2 cm.

Temperatures in Auckland Harbour vary from about 21.8°C to about 11.9°C; nutrient values are highest in summer and lowest in winter (Slinn, 1968). Unfortunately, no data on seasonal abundance of *M. roseus* in the Auckland area are available. Temperatures in Otago Harbour vary from 14–16°C to 6–8°C (Slinn, 1968; Rainer, 1981). Annual temperature range for Cape Farewell, in the far northwest of South Island, is about 10–17°C (Grieg et al., 1988:fig. 5). Thus, across the geographic distribution of *M. roseus* in New Zealand, summer and winter temperatures differ by approximately 7–10°C.

Tasmania

In Tasmania, *M. roseus* occurs from the southern D'Entrecasteaux Channel toward South East Cape, up the east coast to the Furneaux Group islands off northeastern Tasmania in Bass Strait (Figure 1b). It is most common in the D'Entrecasteaux Channel to Tasman Peninsula, but it is also well established in other areas, although records

are sparse. There are no records for southern and western Tasmania, but as very little is known of the marine fauna of this area due to lack of collecting, we cannot confirm or exclude its presence there. *M. roseus* is present but rare in northeastern Tasmania.

Specimens for this study were collected from Tinderbox Cove, at the northern end of the D'Entrecasteaux Channel, opposite North Bruny Island (Figure 1b). The site is a shallow rubble reef, with a steep 3 m wall to a muddy bottom, which then slopes away to over 30 m depth. The animals are found in large numbers on the muddy bottom, particularly at the base of the wall, where the specimens were collected (Figure 3).

The climate in this part of Tasmania is very seasonal. Water temperature in summer (December to about late March) is about 15°C; in winter (late May to about October), it is about 10°C, sometimes even cooler. Tinderbox Cove, as well as most of D'Entrecasteaux Channel, is subject to the influence of meltwater down the rivers, in particular the Derwent and Huon rivers. This cold water

lowers the local water temperature to below that of the nearby open sea (K. Gowlett-Holmes, personal observation).

Discussion

Maoricolpus roseus shows a distinct geographic pattern of abundance around New Zealand. In Auckland and Otago harbours, it is present in densities among the highest recorded for members of its family (Allmon, 1988); it is rare along the northwest coast of South Island, but moderately common along the southern coasts. This pattern does not appear to fit with the correlation observed elsewhere of highest turritellid densities in areas of moderate coastal upwelling (Allmon, 1988), but may be explained by a combination of salinity, food supply, turbidity, and sediment stability.

Powell (1937) noted that salinities in Auckland Harbour were always less than 34.5‰, and he maintained that "lower salinity in the Upper and Inner harbours is the main factor which confines the *Maoricolpus* formation to these areas" (1937:368). Although salinities are also low in Otago Harbour (31.4–34.7‰; Rainer, 1981), where *M. roseus* is also superabundant, the salinity range given by Rainer is for the entire length of the harbor, including the uppermost region where freshwater input has a significant effect. *M. roseus* is apparently most abundant in channels in the middle and outer reaches of the harbor, where the salinity range is smaller. At Portobello on the Otago Peninsula, for example, mean monthly salinity varies from 32.5 to 34.8‰ (Roper & Jillett, 1981).

The common occurrence of *M. roseus* in areas with very coarse or very firm substrates and moderate to strong currents may be due more to the higher suspended food supplies provided by such currents than to any substrate preference. At the same time, this species may prefer areas in which terrigenous sedimentation rates are low. This may explain why *M. roseus* does not appear to be common on the west coast of South Island; the west coast is a shelf characterized by high modern sedimentation, in marked contrast to the Otago–Southland and Northland shelves, which are areas of very low modern sedimentation characterized by coarse sediments with important relict biogenic components (Carter, 1975).

The broad pattern of primary productivity around New Zealand (Bradford, 1980a, b) generally shows higher values off southern, southeastern, and greater Cook Strait regions, whereas lower values tend to be found in the Tasman Sea along the west coast (apart from localized maxima associated with episodic upwelling). There is some understanding of the oceanographic conditions contributing to these patterns. For instance, nutrient enrichment in the region of the Subtropical Convergence Zone around southernmost New Zealand appears to cause high primary and secondary productivity, although with considerable year-to-year variability (Probert et al., 1979; Bradford et al., 1991; Butler et al., 1992). High productivity in the

Golden Bay–Tasman Bay–Marlborough Sounds region, on the other hand, appears to be associated with localized mixing and nutrient upwelling (Bowman et al., 1982; Bradford et al., 1986). Thus, the broad pattern of productivity around New Zealand may have an underlying influence on the distribution of communities in which *M. roseus* is a significant component. Complicating this interpretation, however, is the paucity of distributional data for the species. Furthermore, *M. roseus* is a species of shelf and inshore waters in which productivity may be largely determined by local coastal processes.

LIFE POSITION AND BEHAVIOR

Observations of life position and behavior of *M. roseus* were made at Doubtful Sound and Paterson Inlet, New Zealand by R. Aiello.

Turritellids are basically sedentary suspension feeders, often burrowing in soft substrates with only their apertures exposed (Allmon, 1988; Allmon et al., 1992). They show considerable behavioral heterogeneity, however, often crawling actively and assuming a variety of life orientations. This complexity is well illustrated by *M. roseus* in New Zealand, where a number of individuals were observed in an unusual and puzzling life orientation. In Paterson Inlet, most animals observed were on the sediment surface, aperture down. Several live individuals, however, were oriented vertically, apex down, and buried up to the last 1–2 whorls. Their apertures showed no preferential orientation. At Doubtful Sound, most individuals were again on the sediment surface, most with aperture vertical. A considerable number, however, were apex down in cracks and crevices in the nearby boulders and rocks (Figure 2). A number were wedged into cracks at the base of a sloping rock, apertures facing away from the wall. Almost every crevice contained at least one individual in this orientation, and several had up to three in a row in the same crevice, all more or less the same size. This vertical orientation is apparently identical to that observed in a single living individual of *Turritella gonostoma* in the Gulf of California (Allmon et al., 1992:fig. 2E), but how it is attained and its significance are unclear.

PREDATION

Published information on predation on *M. roseus* is sparse. Red cod (*Pseudophycis bachus*) have been recorded feeding on *M. roseus* in the Otago area (Graham, 1939). King & Clark (1984) recorded *M. roseus* in the diets of rig or smoothhound (*Mustelus lenticulatus*) in Golden Bay (northern South Island).

New observations of predation intensity on living *M. roseus* were made at Doubtful Sound and Paterson Inlet, New Zealand by R. Aiello.

At Groper Island, Paterson Inlet, Stewart Island, the 11-armed starfish *Coscinasterias calamaria* was observed feeding on *M. roseus*. Of 22 live starfish examined on one



Figure 4

Living individual of *Maoricolpus roseus* in grasp of starfish (*Coscinasterias calamaria*) and being attacked by muricid gastropod *Xymene* (*Zeatrophon*) *ambiguus*. Paterson Inlet, Stewart Island, New Zealand. Depth approximately 15 m. Photo taken 21 February 1990. Scale bar = 2 cm.

SCUBA dive, two had individuals of *M. roseus*, nine had unidentified bivalves, and 11 had nothing held in their everted stomachs. In one instance, a starfish was observed holding a turritellid that was also being preyed upon by the muricid gastropod *Xymene* (*Zeatrophon*) *ambiguus* (Philippi) (Figure 4). The turritellid was freed from both predators, and the hole made by the muricid examined by SEM (Figure 5). It is similar to previously described muricid drill holes (e.g., Boucot, 1981:204–207) in having relatively straight, vertical sides.

Predation intensity on *M. roseus* by fish may vary at the two New Zealand study sites. At Doubtful Sound, fish were few, as were missing arm tips on the abundant ophiuroids and crinoids. No living *M. roseus* were seen lacking opercula, and when touched, healthy snails were relatively slow to withdraw into their shells. As mentioned above, aperture orientations were mostly perpendicular to the substrate, with mantle margin exposed. At Stewart Island, in contrast, fish populations were high and fish were feeding actively. Six of the 79 living *M. roseus* examined lacked

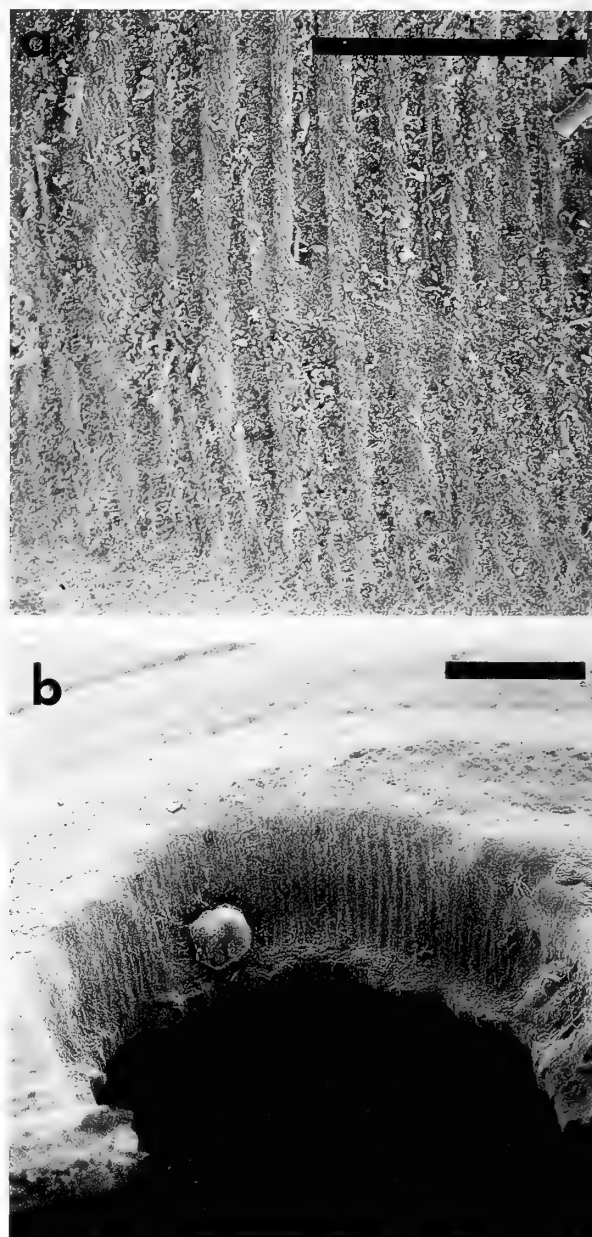


Figure 5

Results of the predation pictured in Figure 4 by the muricid gastropod *Xymene* (*Zeatrophon*) *ambiguus* on *Maoricolpus roseus*: scanning electron micrographs of drill hole made by the muricid in the shell of the turritellid. a. Closeup of radular scratches on the side of hole; b. view of hole in cross-section. Scale bars = 1 mm.

opercula. Most individuals were aperture down with their mantle barely visible, and the animals were very quick to withdraw when touched.

M. roseus appears to have few natural predators in Tasmania. It has been observed being attacked and eaten by

starfish (*Uniophora* sp.) and by several unidentified stingrays. Most of this predation, however, appears to occur on small juveniles, and native predators are apparently not suited to deal with a turritellid of this size. This may explain the almost explosive increase in its numbers in the last 15 years (see below).

Most adult mortality of *M. roseus* in Tasmania appears to occur during storms. In some areas of the D'Entrecasteaux Channel, large numbers of adult *Maoricolpus roseus* are cast up during storms, and can literally be scooped up by the bucketful in some places. Most of the channel is protected from the prevailing winds, but occasional violent southerly storms in the area funnel up the Channel and stir the area around Tinderbox (K. Gowlett-Holmes, personal observation).

INVASION OF TASMANIA

M. roseus was first noticed in Tasmania in the D'Entrecasteaux Channel in the late 1950s when a few isolated specimens were dredged; by the early 1960s, the species was well established and expanding rapidly (Greenhill, 1965). Its mode of introduction is suspected to have been on live oysters (*Tiostrea chilensis* (Philippi) and/or *Crasostrea glomerata* (Gould)) imported from New Zealand. Several other species of New Zealand mollusks and at least one crab were introduced into Tasmania in this way, all initially found only in D'Entrecasteaux Channel and Derwent Estuary area. The venerid bivalve *Venerupis* (*Paphirus*) *largillierii* (Philippi), *M. roseus* and a chiton, *Chiton* (*Amaurochiton*) *glauca*, have become well established and have expanded in range, but most of the other introduced species remain rare, and some may have become extinct since the oyster trade ended.

In the last 30 years, *M. roseus* has become a dominant species in soft bottom areas up the east coast of Tasmania, and was recorded from an island in the Furneaux Group for the first time early in 1992 (K. Gowlett-Holmes, personal observation). Native turritellids, particularly *Gazameda gunnii* (Reeve), have become increasingly rare during the same period. Recent observations in southeastern Tasmania indicate densities of *M. roseus* of more than 100 per m², while live native turritellids are completely absent. There are no quantitative data on *M. roseus* displacing native taxa, only anecdotal reports. In areas near Hobart, however, where *Gazameda gunnii* was once found in reasonable numbers, it is now absent and *M. roseus* is abundant. The timing of the demise of *G. gunnii* corresponds to the rise of *M. roseus*, mainly in the last 20 years. The major effect of *M. roseus* appears to be alteration of the substrate, but there have been no studies testing this hypothesis.

GROWTH

Life span and age of reproduction have been determined by direct observation in only one turritellid species: in the

Australian species *Gazameda gunnii* (Reeve), reproduction begins when the adults are 2.5–3 years of age and is repeated throughout a life span of 6–7 years (Carrick, 1980). Based on size and growth line counts, *Turritella communis* Risso from the northeastern Atlantic may live as long as 10–15 years, but most individuals probably live 2–3 years (see Allmon, 1988).

In the absence of direct observations, indirect methods for assessment of age and growth rate must be used. One such method, analysis of annual variations in stable isotopic composition (¹⁸O/¹⁶O; ¹³C/¹²C) of shell carbonate, was used by Allmon et al. (1992) to assess growth history in *Turritella gonostoma* Valenciennes, 1832 from the Gulf of California. These authors concluded that the individuals examined were no more than 1.5–2.0 years old at the time of collection. We have used the same techniques in the present study on two individuals of *Maoricolpus roseus*.

Materials and Methods

The shells of two specimens of *M. roseus*, cleaned of their soft tissues, were selected for oxygen and carbon isotopic analysis. One specimen was collected from Paterson Inlet, Stewart Island, New Zealand on 20–21 February 1990, and the other from Tinderbox Cove, Tasmania on 24 July 1991. Both specimens were approximately the same size, although the New Zealand specimen was slightly larger and stouter. Both shells are deposited as voucher specimens in the Malacology Collection of the Florida Museum of Natural History, University of Florida (UF), Gainesville, Florida.

The specimen from Tasmania (UF 193555) was 64 mm long and in excellent condition when collected. Twelve whorls were present and, based upon comparison with smaller specimens with complete apices, we estimate that the initial two whorls had been abraded from the apical end. The New Zealand specimen (UF 193556) was 66 mm long and also in fine condition. Ten whorls were present, and we judged that the initial four whorls had been worn from the apex.

Sampling procedures followed those described in Allmon et al. (1992). The sampling yielded 52 separate samples from the New Zealand shell and 55 samples from the Tasmania shell, each spaced about 2–3 mm apart (Figure 6). Each sample of powdered aragonite was cleaned, treated to remove organic material, and reacted with orthophosphoric acid to produce CO₂ gas, according to the procedures detailed in Allmon et al. (1992). The isotopic difference between the derived and purified sample CO₂ gas and the PDB standard was determined with a fully automated, VG Isogas PRISM Series I mass spectrometer, equipped with triple collectors and micro-inlet system, in the Stable Isotope Laboratory of the Department of Geology, University of Florida. All values are reported in the standard (δ) notation where:

$$\delta^{18}\text{O} = [({}^{18}\text{O}/{}^{16}\text{O})_{\text{sample}}/({}^{18}\text{O}/{}^{16}\text{O})_{\text{standard}} - 1] \times 10^3 \text{ per mil (‰)}$$

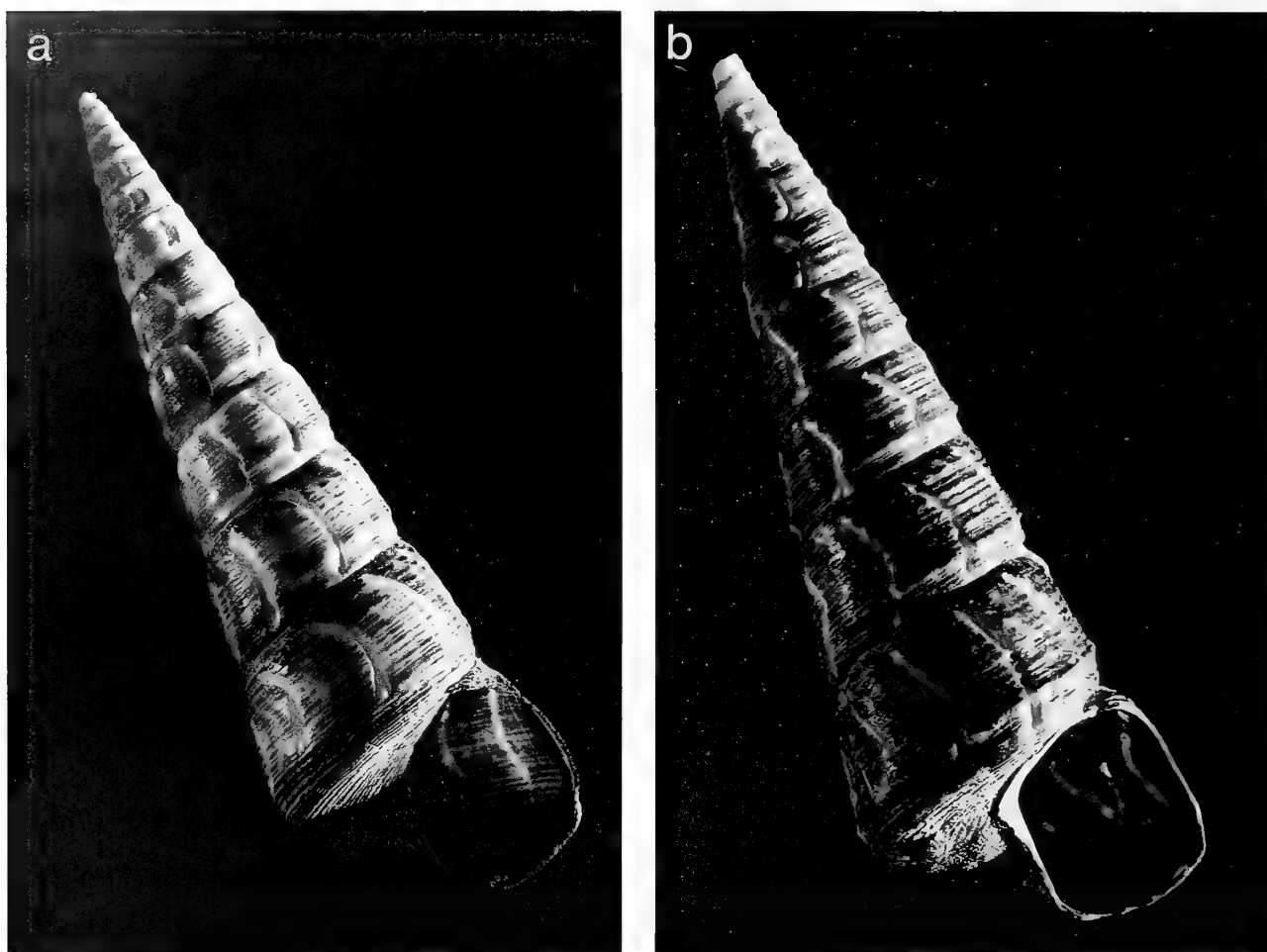


Figure 6

Specimens of *Maoricolpus roseus* used in isotopic analyses of growth. a. Specimen from Tinderbox, Tasmania (UF 193555), 64 mm long; b. specimen from Paterson Inlet, Stewart Island, New Zealand (UF 193556), 66 mm long.

Determinations of $\delta^{13}\text{C}$ were made concurrently with $\delta^{18}\text{O}$. Average reproducibility, as evidenced by duplicate analyses (10% of analyses) and standards run before and after sample strings, was approximately $\pm 0.1\text{‰}$.

Results

The stable isotope records for each specimen are plotted in Figure 7 in standard fashion, with lighter (depleted) values toward the top. This convention derives from paleotemperature interpretations of the isotopic variations (in particular $\delta^{18}\text{O}$) in which warmer temperatures, and their correspondingly depleted isotopic values, are plotted toward the top while cooler temperatures and heavier (enriched) values toward the bottom. The ontogenetic record of isotopic variation is plotted from left (shell apex) to right (aperture). Detailed isotopic profiles were obtained for both shells. As sample spacing remained constant in each, the number of samples per whorl increased toward the aperture, keeping pace with whorl expansion.

The $\delta^{18}\text{O}$ record in the Tasmanian specimen (UF 193555; Figure 7A) is characterized by a strong cyclicity. Three major cycles, interpreted as annual (see below), are evident. The initial cycle is fairly broad, extending from whorls 3–10. The second is also broad but more peaked, ranging from whorls 10–13. The final cycle includes portions of whorls 13–14 and exhibits a reduction in both amplitude and period. This reduction almost certainly reflects an ontogenetic decline in shell growth rate (see Discussion). The overall isotopic amplitude is 1.85‰ ($+0.25$ to $+2.10$) while the mean is $+1.13 \pm 0.39$ (SD). In contrast, the $\delta^{13}\text{C}$ profile shows little or no cyclicity. After an initial enrichment of almost 1.0‰ from whorls 3–7, the carbon isotopic values fluctuate between $+3$ and $+4\text{‰}$ and display a weak ontogenetic trend toward depletion. The mean $\delta^{13}\text{C}$ value is $+3.39 \pm 0.22$. The oxygen and carbon isotopic records in this specimen show no correlation with one another ($r^2 = 0.048$).

The $\delta^{18}\text{O}$ profile for the New Zealand specimen (UF 193556; Figure 7B) does not reveal a conspicuous cyclicity.

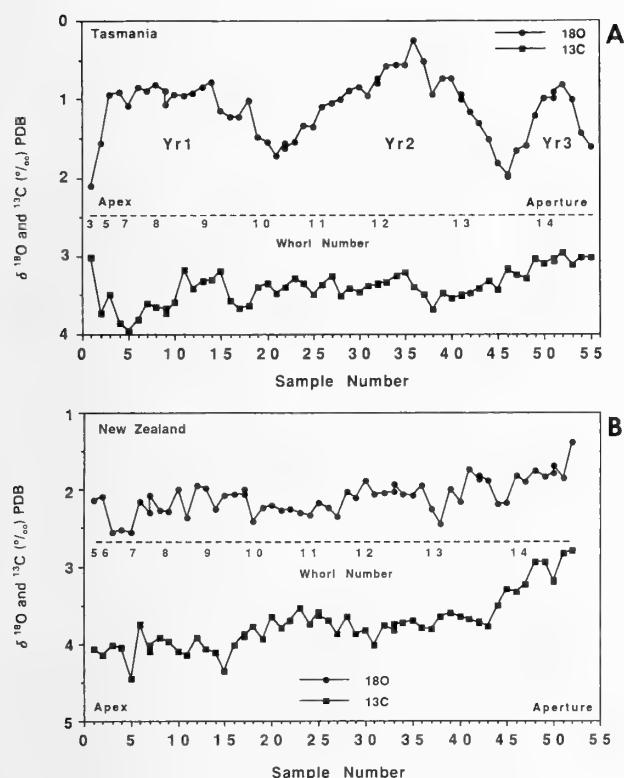


Figure 7

Plots of oxygen and carbon isotope records, relative to the PDB standard, for the two specimens of *Maoricolpus roseus* shown in Figure 6. Results are plotted from the apex (left) to aperture (right). A. Specimen from Tasmania (UF 193555). B. Specimen from New Zealand (UF 193556).

Instead, $\delta^{18}\text{O}$ values fluctuate between about +2 and +2.5‰ over most of the record before tailing off toward slightly lighter values near the end. The overall oxygen isotopic amplitude is 1.19‰ (+1.38 to +2.57), and the mean is $+2.09 \pm 0.23$. The $\delta^{13}\text{C}$ values fluctuate between +3.5 and +4.5‰ across the early whorls (5–10); thereafter, they oscillate between +3.5 and +4.0‰ until sample 44, which begins a depletion trend that characterizes the remainder of the record. The mean $\delta^{13}\text{C}$ value is $+3.74 \pm 0.35$. In this specimen, the oxygen and carbon profiles are very weakly correlated ($r^2 = 0.347$).

Visual comparison of the oxygen isotopic profiles from the two shells reveals significant differences in the pattern of isotopic variation throughout ontogeny (Figure 7). Numerical comparison suggests that the $\delta^{18}\text{O}$ values from the New Zealand specimen are enriched with respect to those from the Tasmania specimen by an average of approximately 1.0‰. This observation is supported by a t-test, which clearly indicates that the mean values from each shell are statistically distinct ($P \ll 0.001$). The pattern of ontogenetic variation is much more similar between the carbon isotopic profiles of the two shells. Here the mean $\delta^{13}\text{C}$ values differ by only 0.35‰, with the New Zealand

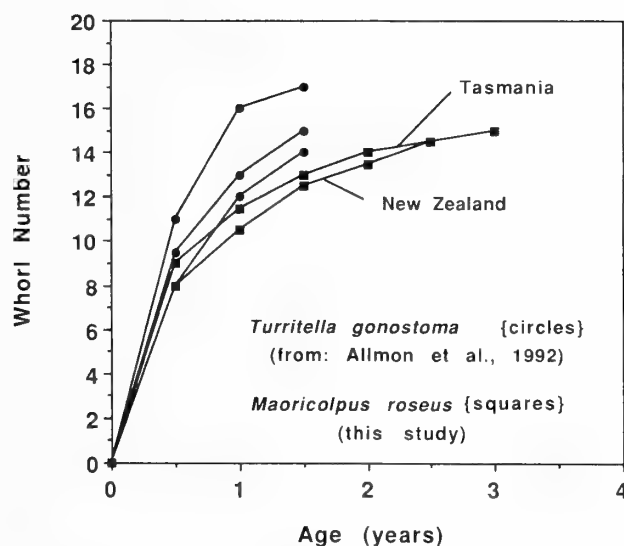


Figure 8

Growth curves (whorl number vs. inferred age) for two *Maoricolpus roseus* specimens pictured in Figure 6 (squares), plotted together with growth curves for three specimens of *Turritella gonostoma* from the Gulf of California (from Allmon et al., 1992) (circles).

shell once again more enriched. Despite these similarities, however, t-tests indicate the mean $\delta^{13}\text{C}$ values are also statistically different ($P < 0.001$).

Discussion

Seasonal cycles in shell $\delta^{18}\text{O}$ records have found wide application in assessing the age and growth rate of many species of mollusks (e.g., Epstein & Lowenstam, 1953; Jones et al., 1983; Krantz et al., 1984; Romanek et al., 1987; Allmon et al., 1992). This results from the fact that the principal influences on shell $\delta^{18}\text{O}$ are few, namely temperature and the oxygen isotope composition of the water (which is generally correlated with salinity), and their seasonal variations are often well constrained.

Carbon isotopic profiles are typically more difficult to interpret, largely because more factors are believed to influence shell $\delta^{13}\text{C}$, including: temperature (Grossman & Ku, 1986); variations in ambient total dissolved carbon (TDC), which can result from changes in productivity (often due to upwelling) (Killingley & Berger, 1979; Krantz et al., 1988) or from freshwater input, mixing, etc. (e.g., Keith et al., 1964; Eisma et al., 1976; Arthur et al., 1983); the contribution of light metabolic carbon from various food sources (Tanaka et al., 1986); shell growth (CaCO_3 formation) rates (Turner, 1982; Jones et al., 1983); and/or other organismal vital effects (Romanek & Grossman, 1989; Wefer & Berger, 1991). This range of potential influences on the isotopic composition often makes it difficult to identify which factors are most responsible for the variation seen in any particular record.

The three cycles in the $\delta^{18}\text{O}$ profile of the Tasmanian specimen (Figure 7A) are best interpreted in terms of the annual cycle of temperature change at the collection site. As noted previously, the marine climate in this part of Tasmania is fairly seasonal with temperatures ranging from about 10°C in the (austral) winter to 15°C in the (austral) summer. Using the aragonite paleotemperature equation of Grossman & Ku (1986), as modified by Hudson & Anderson (1989), it is possible to calculate the approximate range of temperatures represented by the $\delta^{18}\text{O}$ variations in the shell. First, the maximum (winter) and minimum (summer) values from each of the three cycles were averaged to produce better estimates of the long-term yearly range in $\delta^{18}\text{O}$. Substituting these values (+0.6; +1.9; range = 1.3‰) into the paleotemperature equation along with the global mean value for the oxygen isotopic composition of seawater, δ_w , yields minimum and maximum temperatures of 11.5°C and 17.1°C, respectively. Each of these temperatures is just slightly higher than the ca. 10–15°C water temperatures reported for this region, but the magnitude of the seasonal change (5.6°C) is virtually the same.

Unfortunately, year-round monitoring of environmental variables (temperature, salinity, δ_w) at the collection site was beyond the scope of this investigation. All comparisons between isotopic profiles and environmental variables are, therefore, only approximate. With this caveat in mind, the major $\delta^{18}\text{O}$ cycles in the Tasmanian specimen reflect the annual variation rather faithfully. Freshwater runoff, which is known to influence conditions in D'Entrecasteaux Channel to varying degrees, may also play an undetermined, but clearly minor role in shaping the seasonal $\delta^{18}\text{O}$ signature. Nevertheless, the evidence clearly points to the conclusion that this specimen was just completing its third year of life when it was collected in the (austral) late autumn–early winter. The isotopic evidence from the first cycle also suggests that shell whorl formation began in the (austral) late winter–earliest spring. This is consistent with the findings of Pilkington (1974), who observed early eggs inside a specimen of *M. roseus* from New Zealand in September and later-stage eggs inside another individual in March.

In comparison, no unambiguous cycles are evident in the $\delta^{18}\text{O}$ profile of the New Zealand specimen, despite a seasonal temperature regime of 8–15°C in shallow coastal waters (see above). Damping of the normal seasonal $\delta^{18}\text{O}$ cycle in mollusks can result from factors such as upwelling or freshwater runoff, which may affect water temperatures directly or alter the isotopic composition of the water directly (Geary et al., 1992). Without knowing the extent to which these factors operate in Paterson Inlet, it is impossible to interpret the shell $\delta^{18}\text{O}$ record with precision. The $\delta^{18}\text{O}$ values of this specimen, as previously noted, are more enriched than those of the Tasmanian specimen. If these values are interpreted as paleotemperatures, using a modern global average δ_w as before, the range of temperatures would be 8.5–13.7°C with a mean of 10.6°C.

Interpretation of the carbon isotopic profiles is more problematic. The lack of strong correlation between the $\delta^{18}\text{O}$ and the $\delta^{13}\text{C}$ values in each shell indicates that temperature probably has a minimal effect in this case. Without detailed year-round environmental monitoring at Stewart Island, however, it is not possible to isolate the principal influences in these shallow water settings where the local interaction between temperature, salinity, and upwelling is likely to be complex.

A final observation concerning $\delta^{13}\text{C}$ involves ontogenetic trends. Whereas the Tasmanian specimen exhibits a weak trend toward lighter values late in its isotopic record (after sample 38), the trend in the New Zealand specimen (beginning after sample 43) is more pronounced. Such ontogenetic trends toward depletion have been noted in $\delta^{13}\text{C}$ profiles of numerous mollusks (e.g., Keith et al., 1964; Jones et al., 1983; Krantz et al., 1987; Romanek & Grossman, 1989; see also Harrington, 1989; Krantz et al., 1988) where they have been attributed to changes in diet or metabolism with age or the onset of sexual maturity. Most recently, Geary et al. (1992) searched and failed to find such ontogenetic declines in $\delta^{13}\text{C}$ in three strombid gastropods from different localities (although earlier Wefer & Killingley (1980) had reported one strombid with such a pattern). In a previous study of turritellids from the Gulf of California, Allmon et al. (1992:fig. 9A, B) showed two of three specimens that exhibited $\delta^{13}\text{C}$ depletion trends toward the end of their isotopic profiles. The third specimen was the smallest (youngest?) of those sampled and may not have reached sexual maturity. Turritellids do not exhibit determinate growth as do strombids, but only large individuals are found associated with egg masses (Allmon, 1988; Hertz, 1990; Allmon et al., 1992:figs. 2D, 4). Therefore it is possible that $\delta^{13}\text{C}$ depletion is associated with the onset of sexual maturity and concomitant reduction in growth rate (see below) in turritellids; as Geary et al. (1992) state, "clearly more work is required."

The $\delta^{18}\text{O}$ profile of the Tasmanian specimen (Figure 7A) is most instructive for understanding growth rates in these gastropods. The three annual $\delta^{18}\text{O}$ cycles in this specimen were used to construct a growth curve for *M. roseus* in a manner identical to that done previously by Allmon et al. (1992) for *Turritella gonostoma*. This curve is plotted along with those of *T. gonostoma* for comparison (Figure 8). Also plotted is a best estimate of the growth curve for the New Zealand specimen of *M. roseus*. Because this specimen lacks clearly defined $\delta^{18}\text{O}$ cycles, the divisions between years of growth are not obvious. The best estimate was produced by comparing the $\delta^{18}\text{O}$ record with that of the Tasmanian specimen and selecting the most likely inflection points between years, assuming that the growth rates do not differ widely. Samples 18 and 38 were used to demarcate the end of the first and second years, respectively, in the New Zealand specimen.

Growth rates in *M. roseus* are clearly fastest in the first year of life and slow significantly thereafter. As with *Turritella gonostoma*, the most rapid seasonal growth occurs

during the warmest months, particularly in the first year of life. This was suggested by the numerous light $\delta^{18}\text{O}$ values in the first year that represent warmer temperatures. The growth curves also indicate that *M. roseus* grows more slowly than *T. gonostoma* from the Gulf of California, and probably lives longer. Life span in *T. gonostoma* was estimated at 1.5–2.0 years (Allmon et al., 1992), whereas *M. roseus* lives for at least three years and possibly longer. It remains to be determined what factors may be responsible for these differences. The two species may simply have different deterministic life spans and growth rates. Or growth may be related to temperature. Temperatures in the northern Gulf of California vary from approximately 13 to 29°C, although *T. gonostoma* may prefer temperatures around 15–17°C, and may move to track these cooler temperatures during the year (Allmon et al., 1992). The temperatures preferred by *M. roseus* are unknown but based on the isotopic results they may be closer to 12°C.

CONCLUSIONS

1) *M. roseus* appears to prefer areas of coarse to very coarse, or if fine-grained, very firm, substrates, and moderate to strong currents in depths of 1–130 m and temperatures of 8–20°C.

2) Abundance and distribution of *M. roseus* in New Zealand appear not to be strongly correlated with degree of coastal upwelling, but to be positively correlated with availability of suspended food and negatively correlated with amount of suspended terrigenous sediment.

3) In at least one area, living *M. roseus* are often found oriented vertically in rock crevices and shell gravels. This peculiar orientation has also been noted in *Turritella gonostoma* from the Gulf of California, but remains incompletely understood.

4) In New Zealand, *M. roseus* is preyed upon by teleosts and asteroids, but in varying intensity at different locations. In Tasmania, most adult mortality may be due to storms.

5) Following its introduction into Tasmania, probably in the first half of this century, *M. roseus* has increased dramatically in abundance, apparently at the expense of a number of local macrofaunal species, including indigenous turritellids. A lack of appropriate predators in Tasmania may be the chief explanation for this increase.

6) In a manner very similar to that of *T. gonostoma* from the Gulf of California, the $\delta^{18}\text{O}$ profile of *M. roseus*'s shell reflects seasonal temperature changes. The greater seasonal range of temperature at the Tasmanian site produces a stronger cyclicity in the $\delta^{18}\text{O}$ profile than does the weaker seasonal temperature variation at the New Zealand site.

7) The two individuals of *M. roseus* analyzed appear to have been approximately three years old at the time of collection. Given their smaller size, this result indicates that *M. roseus* grows more slowly than does *T. gonostoma* from the northern Gulf of California, perhaps as a consequence of lower temperatures. Both species show marked

reductions in growth rate late in ontogeny, perhaps coincident with sexual maturity.

ACKNOWLEDGMENTS

We are grateful to David Hodell and Jason Curtis for help with isotopic analyses and to Peter Frank and an anonymous reviewer for helpful comments on the manuscript. Field work by R. Aiello in New Zealand was made possible by C. W. Thayer, whose assistance is gratefully acknowledged.

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Defensive "Folding" Response in the Shortfin Squid, *Illex coindetii* (Mollusca: Cephalopoda)

by

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Abstract. The broadtailed shortfin squid, *Illex coindetii*, exhibits two variants of a "riddance" behavior (probably based on a reflexlike stereotyped response) when seized by an experimenter. The behavior depends on where the mantle is clasped. If the whole mantle is clasped, the animal reaches backward dorsally to grab the perceived attacker. A more extreme flexion, "ventral folding," occurs only when the animal is captive at the caudal end of the mantle. This second variant involves strong bending of the elastic inner shell (the so-called pen).

INTRODUCTION

Cephalopods exhibit various reflex behavior patterns that are defensive in function. These reflex behavior patterns, however, may have additional functions, along with a defensive one, so that interpretation is sometimes difficult for the observer. Such ambiguity can be minimized when a distinct action pattern is triggered experimentally by a visual, tactile, or electrical stimulus that is likely to be perceived as "threatening" by the target individual (Dilly, 1972; Young et al., 1982; Boletzky et al., 1992).

The observations reported here represent the extreme situation where the animal is captive as if being seized by

a predator. That some cephalopods can escape from such situations in the sea is indicated by the frequent occurrence of heavily damaged and repaired shells in living *Nautilus* (Arnold, 1985) and *Sepia* (Boletzky & Overath, 1991) and by similar traces in the fossil remains of Jurassic and Cretaceous belemnites (Bandel & Spaeth, 1988; Bandel & Kulicki, 1988).

MATERIALS AND METHODS

Occasional short-term experiments made since 1982 in shipboard and laboratory tanks demonstrated consistent "riddance" responses from adult and subadult *Illex coin-*

Explanation of Figures 1 to 5

Figures 1-5. Adult male *Illex coindetii* (19 cm DML).

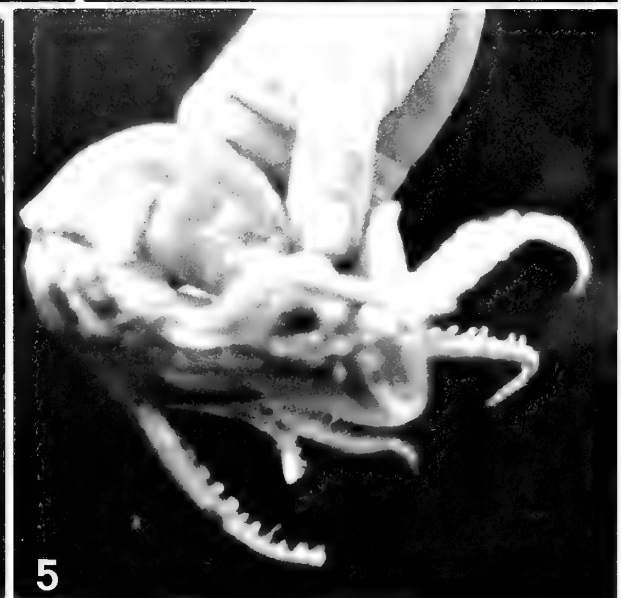
Figure 1. When the whole mantle is clasped by the experimenter, the animal extends the dorsal and dorsolateral arms backward dorsally.

Figure 2. When the caudal end of the mantle is clasped, the animal bends ventrally and extends all the arms and the tentacles backward. Note the left tentacle in advance of the arms, club suckers becoming attached to the fingers of the experimenter.

Figure 3. A few seconds after the situation shown in Figure 2. The tentacle club moves further backward, while the arms become attached to the fingers of the experimenter. Note the deep indentation in the ventral mantle surface.

Figure 4. When the caudal mantle end is held with thumb and forefinger tips only, the animal undergoes bending movements similar to those shown in Figures 2 and 3, and then becomes completely folded, the lateral and ventral arms grasping the mantle end. Note the tentacles extending far beyond the mantle (tentacle clubs at the right side of the picture).

Figure 5. If the arms do not establish contact with the fingers of the experimenter, the animal begins to relax. Note the sharp fold still present in the ventral mantle surface.



detii. To document this, an adult male (19 cm dorsal mantle length) caught in late January 1985 during the CEPHARECH trawling program aboard R/V *Pr. Georges Petit* was used. At that time of year, the aquarium water temperatures were fairly stable at around 12–13°C, i.e., close to the seawater temperatures at a depth of 80–90 meters from which the squid came. For the experiment, the animal was placed in a rectangular 40 liter glass tank with running seawater.

A camera was set on a tripod in front of the tank, at a distance providing for sufficient depth of field. The camera was operated by a shutter release cable with one hand, while the animal was manipulated with the other hand. Black and white photographs were taken in daylight, without a flash.

To avoid unnecessary stress, the animal was released as soon as a complete response was recorded; sessions always lasted less than 20 seconds. Between sessions, the animal was allowed to recover for periods varying from a few minutes to one hour. Normally it settled on the tank floor in a resting position similar to that described in *Illex illecebrosus* (Bradbury & Aldrich, 1969). There were no visible stress effects, and after the 3-hour experiment described here, the animal survived several days in a larger tank. It would not feed regularly, however, and died, probably from starvation, although palaemonid prawn of suitable size were offered *ad libitum*.

OBSERVATIONS AND DISCUSSION

When *Illex coindetii* was grabbed around the whole mantle, it reacted by reaching backward over the head with its dorsal and dorsolateral arms, apparently trying to free itself (Figure 1). This movement is similar to the "dorsal mantle cleaning" observed in cuttlefishes of the genus *Sepia*: *S. officinalis* (Zahn, 1976), *S. orbignyana*, and *S. elegans* (Boletzky, unpublished observation).

A completely different action was triggered by grabbing the caudal mantle end, in the area of the fins (Figure 2). Similar to what occurs in *Sepia* during "ventral mantle cleaning" (Zahn, 1976), the animal bent its head downward and extended its arms and tentacles backward to touch the hand of the experimenter (Figure 3). It is interesting that the tentacles first established contact and "probed" the experimenter's hand (Figure 2), much like the arms which made contact a few seconds later (Figure 3). When the mantle end was held with only two fingertips close to the anterior edge of the fins, the animal grabbed its own "tail," using its lateral and ventral arms; the tentacles were not used and extended far beyond the mantle end (Figure 4). If the arms did not establish contact with the fingertips holding the mantle in front of the fins, the animal released its grip (Figure 5) and slowly unfolded.

What is entirely different from the situation observed in *Sepia*, which has a rigid, calcified inner shell (the cuttlebone), is that *Illex* completely folds when clasp- ing the end of the mantle. This is feasible because the purely

organic "pen" is elastic and does not break during this folding action of the body musculature. Similar folding movements have been observed in a number of other squid (C. F. E. Roper, M. Vecchione, R. E. Young, personal communication). A much more drastic folding of the "pen" occurs in the cranchiid squid *Taonius megalops*, when it rolls up into a ball, the tail being inverted into the mantle (Dilly, 1972).

The apparent "advantage," by contrast with rigid shells, of an uncalcified, flexible shell capable of undergoing strong bending (cf. Hopkins & Boletzky, in press), can be obliterated in relation to positive allometric fin growth. Thus, it is lost at the adult stage in those squid species in which the juvenile fins (in subterminal position) grow into very long, strongly muscular fins, as in *Loligo*. A folding response has apparently never been observed in adult loliginids, although it occurs during early post-hatching life (Boletzky, unpublished observation).

Carefully designed experiments will have to be conducted to analyze the manipulatory capacity of the arms and tentacles once they have taken hold of the noxious agent. Whereas the onset of the folding response suggests a typical reflex action, the subsequent arm movements and sucker actions appear much less stereotyped. Their coordination must be at least as complex under these circumstances as for manipulation in other contexts, namely prey capture and ingestion, male actions during mating and spermatophore transfer, and female actions during egg laying (see Boletzky, 1987, 1993 for reviews).

ACKNOWLEDGMENTS

The Directors of CIRMéd are gratefully acknowledged for making ship time available for the cephalopod sampling program CEPHARECH. Special thanks to the captain and crew of R/V *Pr. Georges Petit* for their excellent collaboration. I am grateful to Dr. Andrew Smith (Chapel Hill and Banyuls) for his critical reading of the manuscript, and to an anonymous reviewer for helpful comments and suggestions.

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Ecological Observations of Two Pleurocerid Gastropods: *Elimia clara* (Lea) and *E. cahawbensis* (Say)

by

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Abstract. The ecology of two pleurocerid gastropods, *Elimia* (= *Goniobasis*) *clara* (Lea) and *E. cahawbensis* *cahawbensis* (Say) was studied in Little Schultz Creek in Bibb County, Alabama. The study area is part of the Cahaba River drainage basin. *Elimia clara* was found in greater proportions in riffle areas of the study stream, whereas *E. cahawbensis* was evenly distributed between riffles and pools. Both species were similar in size-at-hatching and maximum size attained. However, overall mean size differed significantly between the two species, with *E. clara* being the larger of the two. *Elimia clara* and *E. cahawbensis* had similar sex ratios (1.3 males: 1 female) throughout the year. Both species exhibited sexual dimorphism in shell width with females being larger. *Elimia clara* typically had a larger proportion of reproductively active females. Each species maintained greater than 40 percent active females throughout the year, with peak activity in mid to late summer. Both species were mature at 5.5 mm shell width and were iteroparous. *Elimia cahawbensis* had a higher prevalence of trematodes (*Cotylomicrocercus* sp.) than did *E. clara*. Essentially, all infected females were unable to reproduce. Both species of snails had the epizoic red alga, *Boldia erythrosiphon*, but significantly more of the *E. clara* population bore *B. erythrosiphon* than did the *E. cahawbensis* population.

INTRODUCTION

The Pleuroceridae is a rather large family of freshwater prosobranch snails with over 150 species represented in lakes, rivers, and streams across most of North America. Pleurocerids can reach relatively high densities (e.g., Dazo, 1965; Mancini, 1978; Hawkins & Furnish, 1987; Richardson et al., 1988), and in streams may often be the dominant macroinvertebrate (Mulholland et al., 1983, 1985; Hawkins & Furnish, 1987). These snails have a significant

impact on periphyton communities and coarse particulate organic matter (CPOM), which are their primary food resources (Newbold et al., 1982; Gregory, 1983; Hawkins & Furnish, 1987). In addition, pleurocerids may significantly affect nutrient dynamics (Mulholland et al., 1983, 1985), energy flow (Mancini, 1978; Richardson et al., 1988), and may even represent an important renewable substratum for algal attachment (Stock et al., 1987). Despite the apparent ecological importance of the Pleuroceridae, their population biology and ecology has received relatively little attention.

Several studies have examined genetic variation in pleurocerids (e.g., Chambers, 1980, 1982; Dillon, 1988a, b;

Contribution number 204 from the Aquatic Biology Program, the University of Alabama.

Dillon & Davis, 1980), but only a few published studies have addressed their population ecology. Some of these include studies on eggs and egg-laying habits (Jewell, 1931; Van Cleave, 1932; Winsor, 1933), life histories (Magruder, 1934; Dazo, 1965), and population dynamics (Houp, 1970). Others provide age and growth parameters (Stiven & Walton, 1967; Richardson et al., 1988) and reproductive tactics and life-cycle energetics (Aldridge, 1982). These reports are for only a few of the pleurocerids. Such population studies are crucial to understanding a species' life history, how it interacts with its environment, and how it may be influenced by habitat perturbations.

In this study, we provide data on the natural histories of two coexisting pleurocerids, *Elimia* (= *Goniobasis*) *clara* (Lea) and *E. cahawbensis* *cahawbensis* (Say). Both species are limited in distribution to the Mobile River drainage. Monthly density estimates as high as 550/m² and 300/m² have been reported for *E. clara* and *E. cahawbensis*, respectively, with densities lowest in winter and greatest in summer (Richardson et al., 1988). Temporal patterns of biomass for these two species are similar to variation in densities with peaks of about 8.0 g ash-free dry mass (AFDM)/m² and 3.5 g AFDM/m² for *E. clara* and *E. cahawbensis*, respectively (Richardson et al., 1988). Secondary production estimates are similar to those reported for other pleurocerids (Mancini, 1978; Richardson et al., 1988). Size-specific growth rates for both species indicate they may potentially live up to 10 years (Richardson et al., 1988).

MATERIALS AND METHODS

Study site: Snails were collected from Little Schultz Creek in Bibb County, Alabama (T24N, R10E, Sec 30). This small, spring-fed, second-order stream ranges from 1 to 3 m in width (\bar{x} = 2 m) and up to 20 cm in depth and is part of the Cahaba River drainage basin (Richardson et al., 1988). Temperature ranged from 8°C to 24°C with an annual mean of 17.3°C. Alkalinity varied from 55 to 170 mg/L CaCO₃ and pH from 6.8 to 7.7 (Stock et al., 1987). Substratum varied from limestone/dolomite bedrock in riffle areas (current velocity of 25 cm/sec in April 1986) to sand and small cobble in pools (6 cm/sec) (Richardson et al., 1988). Lay & Ward (1987) and Stock et al. (1987) provide detailed descriptions of the study site.

Sampling and parameter estimates: Sampling was described in detail by Richardson et al. (1988). Briefly, snails were sampled randomly, with replacement, using a 0.1 m² box sampler. The sampler was divided into quarters with nylon cord. For each sample, one quarter (0.025 m²) of the box sampler was chosen randomly and used to sample the substrate. Twenty-one such samples were taken each month from February 1985 through January 1986. All snails were removed by hand, and shell width (SW) was measured to the nearest 0.1 mm with a vernier caliper. Maximum and minimum sizes were assumed to be the

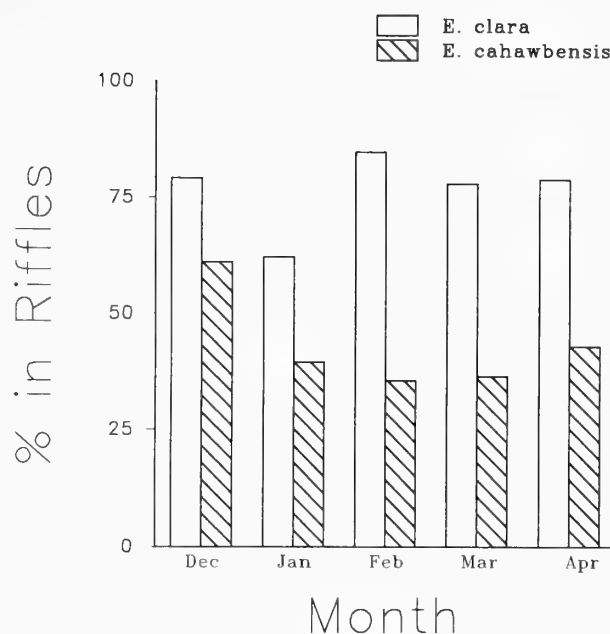


Figure 1

Monthly percentages of *Elimia clara* and *Elimia cahawbensis* found in riffle areas.

size of the largest and smallest individuals, respectively, sampled for each species over the 12 months. Mean size of each species was estimated as the mean shell width of all snails sampled during the study.

Beginning in June 1985, and continuing through April 1986, monthly subsamples of 30 snails each, of *Elimia clara* and *E. cahawbensis*, were randomly chosen. These snails were dissected to determine sex, gonad development of females, and frequency of parasitism by trematodes. The remainder of the collected snails was returned to the stream.

Monthly sex ratios for each species were estimated as the proportion of the 30 specimens (>4.0 mm) that were females (females have an egg-laying sinus on the right side of the foot). Smaller snails have not yet developed external sexual characters. Gonad development of females was determined by examining ovaries with a dissecting microscope ($\times 20$). During gravid periods, ovaries occupy approximately 66 to 75 percent of the uppermost region of the visceral mass, displacing the hepatopancreas. When not gravid, most of the volume is hepatopancreas (Woodard, 1934; Magruder, 1935). This difference allows for a quick and easy estimate of reproductive capability. The proportion of gravid females was determined monthly. During dissection, all snails were scored for presence or absence of trematodes. Monthly prevalence was then determined, but no attempt was made to differentiate among parasite stages (e.g., redia vs. sporocysts).

A different sampling program was used to estimate the prevalence of the epizootic red alga, *Boldia erythrosiphon*

Table 1

Shell widths (SW), percent females, and sex ratios for *Elimia clara* and *E. cahawbensis*. Means are given with SEs and percentages with total number examined.

	<i>E. clara</i>	<i>E. cahawbensis</i>
Maximum/minimum (mm)	9.7/0.8	9.5/0.9
Overall mean ^a		
SW (mm)	6.8 (0.02)	5.9 (0.04)
Male mean ^b		
SW (mm)	6.0 (0.09)	6.5 (0.07)
Female mean ^b		
SW (mm)	7.5 (0.08)	6.8 (0.06)
% female	43.9 (321)	42.9 (324)
Female: male	1:1.3	1:1.3

^a Means are from shell widths of all snails sampled during the study.

^b Means are from snails subsampled for sex determination, reproductive state, and parasitism.

Herndon. Twenty samples (again using the box sampler) were taken monthly from December 1985 through April 1986, when the macroscopic stage of the alga was present. Ten samples were taken from riffles, 10 from pools. Snails were preserved in 95% ethanol and examined for the presence or absence of the alga. Even though other algae were present, *B. erythrosiphon* was, by far, the dominant macroscopic form. Details of sampling were presented by Stock et al. (1987).

Data were analyzed using SAS (1985) with the sub-routines GLM or T-TEST. However, since some of the data were categorical (e.g., sex ratios), the nonparametric replicated goodness of fit test with the G statistic was also used (Sokal & Rohlf, 1981).

Table 2

Monthly mean shell widths of *Elimia clara* and *Elimia cahawbensis*. Means are given in mm with \pm SE and sample size in parentheses.

Month	<i>E. clara</i>	<i>E. cahawbensis</i>
February	6.4 \pm 0.10 (113)	6.1 \pm 0.10 (50)
March	6.5 \pm 0.07 (225)	6.1 \pm 0.07 (159)
April	6.7 \pm 0.08 (163)	5.9 \pm 0.14 (50)
May	6.5 \pm 0.09 (162)	5.8 \pm 0.09 (42)
June	6.7 \pm 0.07 (219)	6.2 \pm 0.09 (68)
July	7.0 \pm 0.06 (223)	6.1 \pm 0.07 (78)
August	7.0 \pm 0.06 (229)	6.1 \pm 0.10 (101)
September	7.0 \pm 0.08 (278)	5.5 \pm 0.20 (98)
October	7.0 \pm 0.09 (245)	5.6 \pm 0.19 (79)
November	7.2 \pm 0.10 (180)	6.1 \pm 0.19 (74)
December	7.2 \pm 0.13 (96)	5.7 \pm 0.29 (41)
January	7.3 \pm 0.10 (145)	5.6 \pm 0.23 (55)

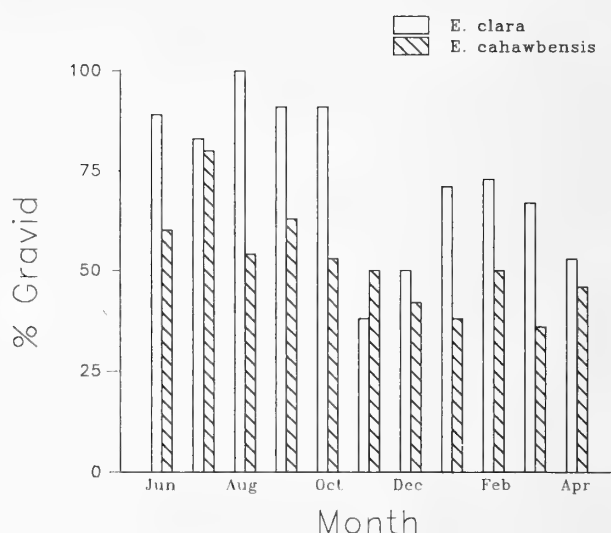


Figure 2

Monthly percentages of gravid females for *Elimia clara* and *Elimia cahawbensis*.

RESULTS

Elimia clara and *E. cahawbensis* had different microhabitat preferences (Figure 1). Overall, *E. clara* was significantly more abundant in riffles than in pools (G test, $P < 0.001$). The proportions of *E. clara* in riffles and pools changed significantly among months (G test, $P < 0.05$ in each case). Conversely, *E. cahawbensis* was found to be randomly distributed among months (G test, $P < 0.05$) and each month (G test, $P < 0.05$).

Elimia clara and *E. cahawbensis* grew to similar shell widths, and the smallest individuals obtained in samples (0.8 mm and 0.9 mm SW for *E. clara* and *E. cahawbensis*, respectively) were similar (Table 1). However, among all samples (including juveniles), *E. clara* had a significantly larger mean shell width than *E. cahawbensis* (ANOVA, $P < 0.0001$). Furthermore, size differences persisted between species even for sexes. Both male and female *E. clara* were larger than their *E. cahawbensis* counterparts (ANOVA $P < 0.05$). The mean shell width of both species changed significantly among months (ANOVA, $P < 0.0001$), and there was a significant species \times month interaction (ANOVA, $P < 0.0001$). Mean shell width of *E. clara* slowly increased over the year, while *E. cahawbensis* oscillated about its annual mean (Table 2).

Sex ratios did not change significantly among months for either species over an 11 month period. In addition, the two species did not differ in percent females among months (G test, $P > 0.05$) or overall (G test, $P > 0.05$; Table 1). On average, both *Elimia clara* and *E. cahawbensis* had significantly more males than females (G tests, $P < 0.05$ for *E. clara* and $P < 0.025$ for *E. cahawbensis*) with 1.3 males to each female (Table 1). Overall, both species exhibited sexual dimorphism in mean shell width, with

females being significantly larger than males (t tests, $P < 0.001$ for *E. clara* and $P < 0.01$ for *E. cahawbensis*; Table 1).

The proportion of gravid females differed significantly between the two pleurocerids among months (G test, $P < 0.01$). *Elimia clara* had a significantly larger portion of mature females gravid than *E. cahawbensis* for all months except July, November, December, and April (G test, $P < 0.005$, Figure 2). Percent of gravid females peaked in July for *E. cahawbensis*, one month earlier than *E. clara* (Figure 2). Hatchlings appeared in low numbers from June through early September. Both species were essentially the same size at onset of maturity, with the smallest gravid females having shell widths of 5.6 and 5.5 mm for *E. clara* and *E. cahawbensis*, respectively. The size of gravid females ranged from the above minima up to the maximum sizes attained by both species.

Elimia clara and *E. cahawbensis* differed in prevalence of trematodes (*Cotylomicrocerus* sp.). On average, *E. cahawbensis* had significantly higher prevalence (G test, $P < 0.001$) than *E. clara* (Table 3). Furthermore, a significantly larger proportion of the female *E. cahawbensis* was infected with parasites than female *E. clara* (G test, $P < 0.005$; Table 3). The proportion of females infected did not vary significantly with time for either species (G tests, $P > 0.05$ for *E. clara* and *E. cahawbensis*). Essentially 100 percent of the infected females of both species were castrated and therefore not gravid. The mean shell widths of infected individuals were 6.8 mm (± 0.30 SE) and 6.9 mm (± 0.08 SE) for *E. clara* and *E. cahawbensis*, respectively, and did not differ between the species (t test, $P > 0.05$).

Both *Elimia clara* and *E. cahawbensis* had the epizoic red alga, *Boldia erythrosiphon* from December 1985 through April 1986. Overall, *E. clara* had a significantly larger percentage (66%) of the population with the attached alga than did *E. cahawbensis* (25%) (G test, $P < 0.001$; Table 3).

DISCUSSION

The two species clearly had different microhabitat preferences. *Elimia clara* was found mostly in riffles, while *E. cahawbensis* seemed to be randomly distributed between riffles and pools. This agrees with Dazo's (1965) and Mancini's (1978) reports for *E. livescens* (Menke) and *E. semicarinata* (Say), respectively. Why *E. clara* prefers erosional areas is not clear. Sampling did not take into account substratum specifics or food resources, either of which may have been the reason for the observed preference.

Elimia clara and *E. cahawbensis* differed in mean shell width even though there was considerable overlap in size (i.e., they hatched and grew to similar sizes). What was responsible for the different size distributions is unclear, but *E. clara* did grow more slowly and exhibit a somewhat longer life span. Whether this difference is of any importance remains to be seen. Snail size has been shown to be important in at least one other pleurocerid. Smaller *E.*

Table 3

Percent (with total number examined) of *Elimia clara* and *E. cahawbensis* with trematodes (populations and females) and the epizoic red alga, *Boldia erythrosiphon*.

	% population with trematodes	% females with trematodes	% with alga
<i>E. clara</i>	5.5 (330)	3.4 (141)	66.4 (538)
<i>E. cahawbensis</i>	27.0 (330)	34.9 (139)	24.7 (162)

clavaeformis suffered weight loss when forced to share food resources with larger snails (Steinman, 1991). Conversely, smaller *E. clavaeformis* escaped burial after simulated flooding more frequently than did larger ones (A. J. Stewart, unpublished data, Oak Ridge National Laboratory). Both *E. clara* and *E. cahawbensis* attained maximum shell widths 3 mm larger than those reported by Stiven & Walton (1967) for *E. proxima*.

Elimia clara and *E. cahawbensis* both displayed significant seasonal changes in size. For *E. clara*, minimum mean shell width gradually increased from February through January with the sharpest break in mean size coming in mid-winter. Because the number of individuals sampled in the largest size classes fell off between January and February, this pattern may be due to a combination of mid-senescence of older, larger individuals in the population and from growth of smaller individuals throughout the remainder of the year. Conversely, minimum shell width of *E. cahawbensis* was observed in late summer and early fall when the number of young of the year (<3 mm) sampled was greatest. There was no discernable decrease in the larger individuals of *E. cahawbensis* at any time of the year.

The sex ratios of *Elimia clara* and *E. cahawbensis* in Little Schultz Creek were both biased toward males. Previously reported sex ratios for various pleurocerids have ranged from 1:1 up to 6.6 females for each male. (e.g., Dazo, 1965; Mancini, 1978; Aldridge, 1982). To our knowledge, this is the first report for pleurocerids indicating a sex ratio significantly skewed in favor of males. This may have been due to our including juvenile females with the males since the two are indistinguishable. However, sex ratios among pleurocerid snails are highly variable and often differ from the expected 1:1 ratio.

It is commonly known that female prosobranchs are typically larger than males (Fretter & Graham, 1964). Females of both *Elimia clara* and *E. cahawbensis* have wider shells on average than males. Why such disparity in size between sexes exists among the prosobranchs is not known but these differences are usually attributed to females living longer than males or to reproductive needs of females (Brown & Richardson, 1992).

The time of year when the largest proportion of females in the population was gravid was taken to be the peak of

the reproductive season. *Elimia cahawbensis* peaked in July, while *E. clara* did not peak until August. These peaks are similar to those found for other pleurocerids (e.g., Magruder, 1934; Woodard, 1934; Dazo, 1965; Mancini, 1978; Aldridge, 1982). Except for four months of the study, *E. clara* always had a larger proportion of gravid females than *E. cahawbensis*. A large number of gravid females was found in both populations all year. This contradicts other studies and may have been because the snails in this study were the most southerly located pleurocerids studied so far.

Both species initiated gonad development at approximately the same size and at sizes similar to *Elimia livescens* (Dazo, 1965). In *Elimia*, onset of maturity may be size-rather than age-related, because many mature at similar sizes, but are different ages. For example, by applying annual mean size-dependent growth rates of laboratory and on-site caged snails (Richardson et al., 1988), it was estimated that *E. clara* may be approximately three years of age when maturing at 5.5 mm. *Elimia cahawbensis*, however, may be 4–4.5 years of age when it reaches maturity at 5.6 mm. Both of these estimates exceed previous reports for pleurocerids by one to two years (Dazo, 1965; Mancini, 1978; Aldridge, 1982). It should, however, be noted that, in this study, the procedure used to estimate age assumed that all snails of a given size grew at a similar rate and would therefore be the same age. Violation of this assumption might reduce the age of individuals of a given size and thereby lower the estimated age at maturation for *E. clara* and *E. cahawbensis*.

Individuals of both species were found to be gravid over a wide size range (approximately 5.5 to 9.5 mm for both species) and therefore, presumably a wide age range. In addition, except for parasitized individuals, essentially 100 percent of the females in the larger size classes were gravid during the peak of the reproductive season. These observations suggest that these pleurocerids may mature at an early age and reproduce each year of their adult life (iteroparity). Both iteroparity and semelparity have been reported in other pleurocerids (Dazo, 1965; Aldridge, 1982).

The Pleuroceridae, especially *Elimia*, have long been known as hosts for many different digenetic trematodes (Dazo, 1965). However, prevalences as high as those found here for *Elimia cahawbensis* are rare. Most published infection levels range from 2 to 20 percent, similar to that reported here for *E. clara*. On average, 35 percent of all mature *E. cahawbensis* females were infected. Because almost 100 percent of these infected females were castrated and therefore incapable of reproduction, parasites may play an important role in population regulation of *E. cahawbensis*. Exactly why *E. clara* had a lower infection rate than *E. cahawbensis* is not known. However, if the ability of miracidia to locate and infect a potential host is inversely related to current, then the microhabitat preference of *E. clara* (riffles over pools) may provide a refuge from parasitism.

The occurrence of *Boldia erythrosiphon* on pleurocerids has previously been reported (Stock et al., 1987 and references therein). It appears that the differential occurrence of the alga (Table 3) may also be attributed to the snails' microhabitat preferences; the alga is most abundant on *Elimia clara* because the snail is more abundant in the microhabitat preferred by the alga (Stock et al., 1987). Interestingly, this commensal relationship may also be a mutualistic one, benefiting the snail. *Elimia clara* may be less vulnerable to predation because of the alga. The alga may have a cryptic effect and camouflage the snail, or the alga may be unpalatable to the snails' predators. However, the alga may also have a detrimental effect on *E. clara*. Because the alga grows in large tufts, the snail may be faced with increased drag during spates.

The population biology and natural history of many stream pleurocerids is still largely uninvestigated. However, if generalizations can be made, it seems they possess a variety of life history patterns, and their population dynamics and species interactions may be further complicated by such factors as commensalism and parasitism. More information is needed on species and trophic interactions and the effects of commensals and parasitic relationships upon the population dynamics of pleurocerids before we can fully understand their role in stream ecosystem processes.

ACKNOWLEDGMENTS

We greatly appreciate the help and guidance of Dr. M. S. Stock in the alga portion of the study and Dr. K. Corkum for identification of the trematodes. We thank Drs. A. C. Benke, S. Harris, and G. M. Ward for comments and discussion. We thank Drs. K. M. Brown and J. E. Alexander, Jr. who reviewed and commented on an earlier version of the manuscript. This study was part of an M.S. thesis completed at the University of Alabama by the senior author.

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Review of the Genus *Placiphorella* Dall, 1879, *ex* Carpenter MS (Polyplacophora: Mopaliidae) with Descriptions of Two New Species

by

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Abstract. The genus *Placiphorella* Dall, 1879, *ex* Carpenter MS is reviewed. Nine species are recognized: *P. velata* Dall, 1879, *ex* Carpenter MS; *P. rufa* Berry, 1917; *P. blainvilliei* (Broderip, 1832); *P. mirabilis* sp. nov.; *P. hanselmani* sp. nov.; in the eastern Pacific, *P. borealis* (Pilsbry, 1892); *P. stimpsoni* (Gould, 1859) and *P. boreali-japonica* Saito & Okutani (1989) in the western Pacific; and *P. atlantica* (Verrill & Smith, 1882) a bathyal-abyssal, cosmopolitan species. Each species is described and illustrated, and its habitat and distribution are discussed. The conspecificity of *P. atlantica* and *P. pacifica* Berry, 1919, is demonstrated, and its broad geographic distribution is discussed.

INTRODUCTION

The genus *Placiphorella* Dall, 1879, *ex* Carpenter MS is unusual among chitons in having a broad anterior expansion of the girdle, a relatively small foot and a modified pallial fold. In these features it is similar to genera in two other families, namely *Craspedochiton* Shuttleworth, 1853 (Cryptoplacidae), and *Loricella* Pilsbry, 1893 (Schizochitonidae), as noted by Saito & Okutani (1992). These modifications reach their greatest development in *Placiphorella* in the form of precephalic tentacles, which facilitate the active trapping and manipulation of live prey (McLean, 1962). The underside of the "head flap" in living animals of *P. velata* and *P. borealis* is brightly colored, with blotches of reddish or purple, and may act as a lure for prey. In addition to the trapping method of feeding, *Placiphorella* species also graze on encrusting sponges, bryozoans, hydroids, compound ascidians, and (rarely) certain types of algae. The setae of most species of *Placiphorella* are host to several species of sessile foraminifera, some of which may be host-specific.

The last review of the genus as a whole was that of Pilsbry (1893). At that time, five species were considered to be members: *Placiphorella velata* Dall, 1879, *ex* Carpenter MS; *Chiton stimpsoni* Gould, 1859; *Placiphorella*

borealis Pilsbry, 1893; *Chiton blainvilliei* Broderip, 1832; and *Chiton petasus* Reeve, 1847. *Placophora* (*Euplacophora*) *atlantica* Verrill & Smith, 1882, was considered by Pilsbry to be a member of the genus *Placiphora* Gray, 1847 (subgenus *Placophoropsis* Pilsbry, 1893).

Thiele (1909) listed *Chiton blainvilliei*, *C. stimpsoni*, and *C. petasus* as members of *Placiphorella*, *sensu stricto*, and *Placophora atlantica* as a member of the subgenus *Placophoropsis*, but made no mention of *Placiphorella velata* (type species of the genus), or *P. borealis*. Recent authors have followed Thiele's revision, except with regard to *Chiton petasus*, which is now known to be in the genus *Craspedochiton* Shuttleworth, 1853.

The present paper recognizes nine species, five in the eastern Pacific Ocean, three in the western Pacific Ocean, and one cosmopolitan. This review focuses primarily on the eastern Pacific species. The western Pacific species, which have been recently revised by Saito & Okutani (1989), are discussed briefly (except for *Placiphorella borealis* Pilsbry, 1892, which is included in the present review because of its presence in the Aleutian Islands), and the reader is referred to the aforementioned paper. Two new species, which previously were confused with *P. velata* and *P. stimpsoni*, are described. The morphological characters of each species are described and illustrated, and nomenclatural confusion is clarified by critical examination of type material, as well as several hundred additional specimens from throughout the geographical range of each species.

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MATERIALS AND METHODS

Live animals were collected by hand intertidally by SCUBA in shallow water (1–30 m) and by dredging and trawling in deeper water (30–300+ m). Whole animals were preserved dry with glycerin using a slightly modified version of the method of Hanselman (1970). Animals were killed by submersion in hot water (>38°C) for several minutes, fixed in 50% isopropanol (or, when available, ethanol) for 5–6 days, then transferred to the alcohol/glycerin solution for final preservation. This method was used because it reduces the amount of storage space required. A few specimens of each species were disarticulated for study of the interior characters of the valves.

Radulae were extracted after dissolution of tissue in 10% KOH at room temperature. The radular ribbons were washed in distilled water, dehydrated in an acetone series, air-dried, mounted on stubs with a thin smear of colloidal silver paint, and sputter-coated with gold.

Setae were removed from preserved specimens and prepared in the same manner as the radulae. Setae and radula specimens were examined at 5 or 10 kv, with an Hitachi S-2100 scanning electron microscope at the Biology Department of Southern Oregon State College (Ashland, Oregon).

Abbreviations of institutions used in the text are as follows. ANSP, Academy of Natural Sciences, Philadelphia; BMNH, the Natural History Museum, London; CAS, California Academy of Sciences, San Francisco; LACM, Los Angeles County Museum of Natural History; LACMIP, Invertebrate Paleontology collection of LACM; NMFAB, National Marine Fisheries Service, Auke Bay Fisheries Laboratory, Auke Bay, Alaska; RBCM, Royal British Columbia Museum, Victoria; RMNH, National Museum of Natural History, Leiden; RNC, the private collection of the author; SBMNH, Santa Barbara Museum of Natural History; UAF, University of Alaska Museum, Fairbanks; UCD, University of California, Davis, Geerat Vermeij Collection; USNM, United States National Museum of Natural History, Washington, D.C.; ZIAS, Zoological Institute, Academy of Sciences, St. Petersburg.

SYSTEMATICS

Polyplacophora Blainville, 1816

Neoloricata Bergenhayn, 1955

MOPALIIDAE Pilsbry, 1893

Placiphorella Dall, 1879, ex Carpenter MS

Type species: *Placiphorella velata* Dall, 1879, ex Carpenter MS by original designation.

Synonyms: *Placophoropsis* Pilsbry, 1893 [type by subsequent designation *P. atlantica* Verrill & Smith, 1882]; *Langfordiella* Dall, 1925 [type by original designation *L. japonica* Dall, 1925 (= *Chiton stimpsoni* Gould, 1859) (Saito & Okutani, 1989)].

Small to medium size chitons, round to oval in outline. Valves very wide and short; lateral areas usually well defined. Articulamentum white to blue-green; head valve with (normally) eight slits; intermediate valves with one slit per side; tail valve with one slit on each side (sometimes obsolete), separated by a caudal sinus. Girdle broadly extended anteriorly and bearing scaled bristles (resembling snakeskin). Pallial fold modified anteriorly into numerous fingerlike extensions (precephalic tentacles). Radula with tricuspid major lateral teeth.

Placiphorella velata Dall, 1897, ex Carpenter MS

(Figures 1–3, 26, 27)

Placiphorella velata Carpenter MS, Dall, 1879:298, pl. 2, fig. 36; Pilsbry, 1893:306, pl. 66, figs. 6–12; Pilsbry, 1898:288; Berry, 1907:52; Berry, 1917a:241; Chace & Chace, 1919:43; Dall, 1921:196; Berry, 1922:453, pl. 3, figs. 13–15; Oldroyd, 1927:315 [917]; Johnson & Snook, 1927:566, fig. 667; Chace & Chace, 1933:123; Leloup, 1942:11, fig. 4; Smith & Gordon, 1948:206; Berry, 1951:214; Smith, 1960:62, fig. 40; McLean, 1962:23, figs. 1–2; Burghardt & Burghardt, 1969:34, pl. 4, fig. 70; Thorpe (in Keen), 1971:882 (in part), fig. 50; Abbott, 1974:403, fig. 4737; Burghardt, 1979:10; Kaas & Van Belle, 1980:137; Putman, 1980:32; Clark, 1982:152; Clark, 1983a:11; Kozloff, 1987:189, fig. 11.13; Baxter, 1987:106; Saito & Okutani, 1989:209; Skoglund, 1989:86 (in part); Clark, 1991:96; Anderson, 1992:205.

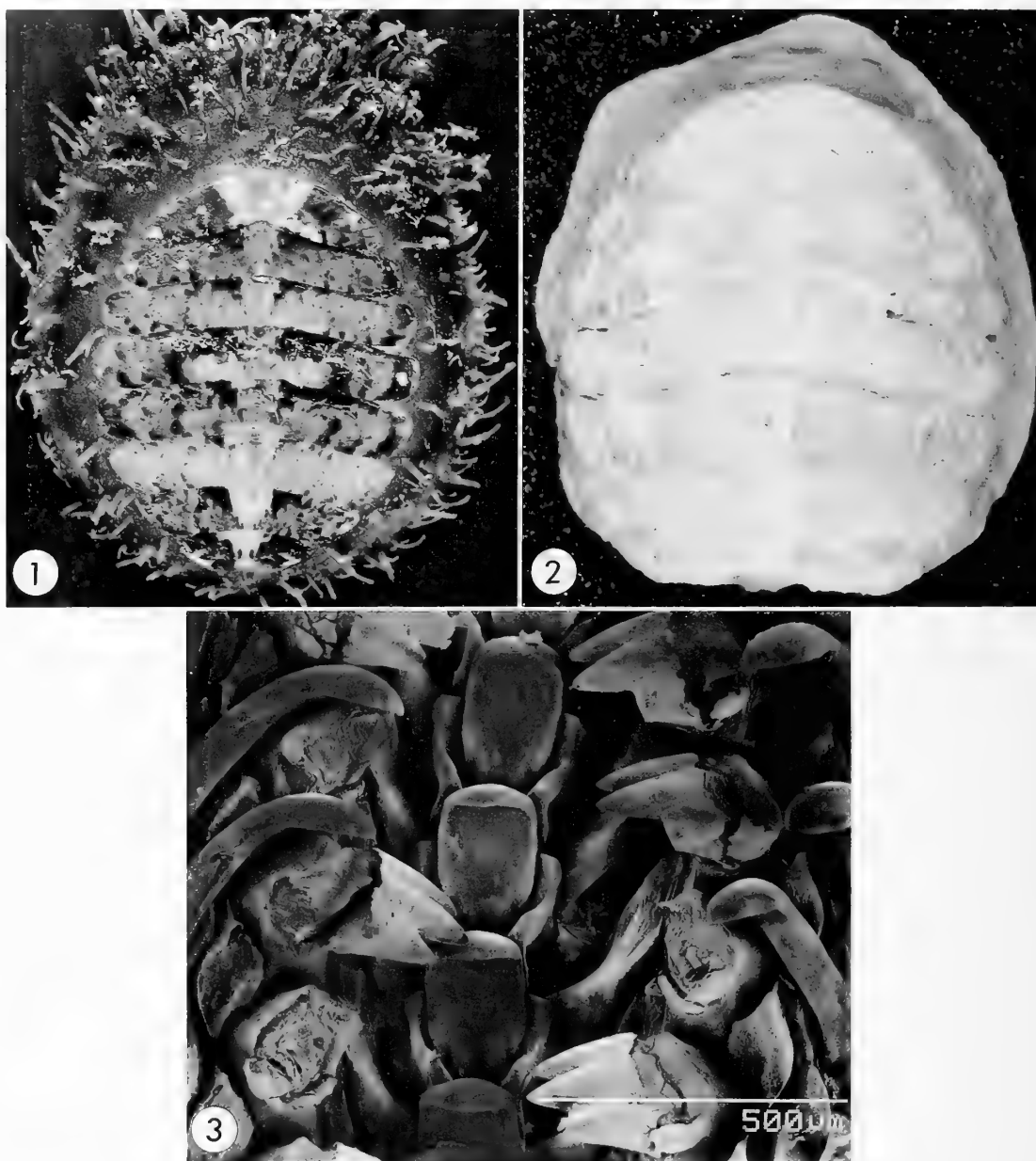
Placiphorella stimpsoni (Gould) Dall, 1921:197 (in part); Oldroyd, 1927:316 [918]; Burghardt & Burghardt, 1969:35 (in part); Putman, 1980:132 (in part); Baxter, 1987:106. *Non Chiton stimpsoni* Gould, 1859.

Placiphorella sp. Kohl, 1974:214.

Diagnosis: Chitons of medium size (to 6.0 cm), round to oval in outline; valves streaked with brown, buff, pink, blue, and olive. Girdle covered with setae of several sizes, clothed with mammillated scales 190–200 μ m in length and 40–45 μ m in width. Rachidian tooth of radula oblong in outline, sides nearly straight, and distally arched; 225–230 μ m in length and 155–160 μ m in width.

Description: Body (Figure 1), broadly oval in outline, valves depressed, subcarinate, side slopes nearly straight to convex, surface of valves microgranular; color brown to chestnut, streaked with buff, pink, blue, and olive. Girdle widely extended anteriorly, covered with rather short, stiff setae, uniform light brown, brown or olive in color. Lectotype (Figure 2) 44.5 mm \times 38.0 mm \times 13.0 mm (slightly contracted). Largest specimen examined (RNC 367d) 61.0 mm \times 44.5 mm \times 10.0 mm (Neah Bay, Clallan County, Washington).

Valves: Head valve crescent-shaped, anterior slope concave in young, strongly convex in very old specimens, with small, rounded notch at apex; tegmental surface sculptureless except for concentric growth lines; interior smooth, strongly thickened anteriorly; insertion teeth short and thick; slits generally eight but occasionally more due to splitting; slit rays faint in young, inconspicuous adults.



Explanation of Figures 1 to 3

Placiphorella velata Dall, 1879, ex Carpenter MS.

Figure 1. Whole animal, RNC 376. Brookings, Curry County, Oregon. 33.0 mm × 28.0 mm.

Figure 2. Lectotype, ANSP 35756. Todos Santos Bay, Baja California, Mexico. 44.5 mm × 38.0 mm.

Figure 3. Radula, RNC 367. Neah Bay, Clallam County, Washington, 1 m.

Intermediate valves very wide and short, oblong in outline, unbeaked, marked by concentric growth lines; lateral areas well defined, raised and slightly depressed medially; central areas often with a false beak (a narrow forward projection at the dorsal ridge); interior smooth with transverse callus extending from center to near the slits; slit rays inconspicuous; sutural laminae very wide, thick, with

a nearly straight and sharp anterior edge, separated by a relatively narrow jugal sinus; insertion plates short and thick, but extending well beyond the narrow eaves.

Tail valve small, depressed; mucro posterior, recurved and elevated; posterior margin indented; sutural laminae broad, truncated anteriorly, separated by a narrow sinus; insertion teeth very short and thick; interior with thick,

transverse callus, extending (and narrowing) from center to near tips of sutural laminae; one (rarely two or more) slits per side, separated by a shallow caudal sinus.

Girdle: Wide, broadly extended anteriorly and covered with large, scaled setae (Figure 26). Scales (Figure 27) rather elongate, about 190–200 μm in length and 40–45 μm in width, proximally pointed, distally rounded, with a small spicule at the tip; and scattered, very minute, pointed scales about 25 μm in length. Margin of girdle with slender, pointed spicules about 145 μm in length.

Pallial fold strongly developed, incised posteriorly, modified anteriorly into 16–22 fingerlike projections (prephallic tentacles). Gills nearly holobranchial, extending from anterior margin of valve ii to posterior margin of valve vi, about 18–22 per side in specimens over 20 mm in length.

Radula (Figure 3): With about 42 rows of mature teeth (in specimen 27 mm in length [RNC 367a]); rachidian tooth oblong in outline, sides nearly straight, top slightly arched; basal portion abruptly constricted and somewhat thickened, about 225–230 μm in length and 155–160 μm in width; minor lateral teeth roughly triangular, with a centro-lateral spur, thickened from the base to the antero-lateral corner, about 230 μm in length; spatulate uncinial teeth relatively thick and narrow, about 395 μm in length.

Type locality: Todos Santos Bay, Baja California, Mexico (31°53'N, 116°32'W).

Type material: ANSP 35756: **Lectotype** (largest specimen) and two **paralectotypes** (herein designated) [leg. Joseph Jeans (*ex* H. Hemphill)].

Additional material: ALASKA: 1 specimen, LACM 141156; 1, RNC 220, English Bay, Hichinbrook Island, Prince William Sound; 3, RNC 236, Saint Lazaria Island, Sitka Sound; 1, RNC 505, Dall Island. BRITISH COLUMBIA, CANADA: 3, RNC 335, Sooke, SW Vancouver Island; 1, RBCM 980-331-6, Cape Perkins, Quatsino Sound, Vancouver Island, 11 m. WASHINGTON: 37, RNC 367, Neah Bay, Clallan County. OREGON: 1, RNC 27, Sunset Bay, Coos County; 1, RNC 961, Island Rock, SW of Port Orford, Curry County, 19 m; 12, RNC 376, Brookings, Curry County. CALIFORNIA: 3, CAS 017676, Patricks Point, Humboldt County, 0–1 m; 4, CAS 017666, Salmon Creek (mouth), Mendocino County, 0–1 m; 3, RNC 1121, Monterey Bay, 5–6 m; 1, CAS 017674, Deadman Island, San Pedro Bay, Los Angeles County. MEXICO: 2, CAS 075733, Bahía Puerto Escondido, Baja California Norte, 6 m; 1, LACM 51-16.1, 16 km W of Punta Malarrimo, Baja California Sur; 1, LACM 71-14.41, E side of Punta Entrada, at Sail Rock, N entrance to Bahía Magdalena, Baja California Sur; 1, LACM 71-14.41, E side of Punta Entrada, at Sail Rock, N entrance to Bahía Magdalena, Baja California Sur, 3–15 m.

Distribution: *Placiphorella velata* ranges from south-central Alaska to central Baja California, but it is very rare north of Vancouver Island. The northernmost record is English Bay, Hichinbrook Island, Prince William Sound,

Alaska (60°17'05"N, 146°40'07"W) (LACM 141156). The southernmost record is E side of Punta Entrada, at Sail Rock, N entrance to Bahía Magdalena, Baja California Sur, Mexico (24°32.4'N, 112°04'W) (LACM 71-14.41).

Habitat: *Placiphorella velata* is found from 0–20 m, under ledges and in crevices, on the tops, sides, and bottoms of cobbles and boulders, and in sea urchin (*Strongylocentrotus purpuratus*) excavations in bedrock, mostly in areas of light to moderate wave action or tidal flow.

Fossil record: An intermediate valve of *P. velata* has been found in the Pleistocene deposits at First Army terrace, Army Camp Beach, San Nicolas Island, California (LACMIP loc. 11004), and Hilltop Quarry (upper sand facies), Los Angeles County, California (SBMNH 35631).

Remarks: *Placiphorella velata* has been confused with *P. stimpsoni* (Gould, 1859), *P. hanselmani*, and *P. mirabilis*. Recently however, *Placiphorella stimpsoni* has been shown to be restricted to the waters of Japan (Saito & Okutani, 1989) and Korea (Dell'Angelo et al., 1990). Comparisons to *P. hanselmani* and *P. mirabilis* are included under those species. The type specimens of this species were originally syntypes, and as yet have not been recatalogued (D. Vardes, personal communication, May 1994).

Placiphorella atlantica (Verrill & Smith, 1882)

(Figures 4–8, 28, 29)

Placophora (*Euplacophora*) *atlantica* Verrill & Smith, 1882: 365; Verrill 1884:206, pl. 30, figs. 1–1b.

Chiton coronatus Fischer MS, Locard, 1898:100, pl. 4, figs. 22–25.

Placophoropsis atlantica (Verrill & Smith), Pilsbry, 1893:313, pl. 65, figs. 73–75, pl. 66, figs. 18–24; Leloup, 1942: 14–15, pl. 1, fig. 4, pl. 2, fig. 1a–d.

Plaxiphora atlantica (Verrill & Smith), Johnson, 1915:10; Dautzenberg, 1927:231; Burghardt, 1979:12.

Placiphorella borealis Pilsbry, Berry, 1917b:13, pl. 8, figs. 3–5, pl. 10; Abbott, 1974:403; fig. 4739; Putman, 1980: 133, figs. 65–67. *Non Placiphorella borealis* Pilsbry, 1893.

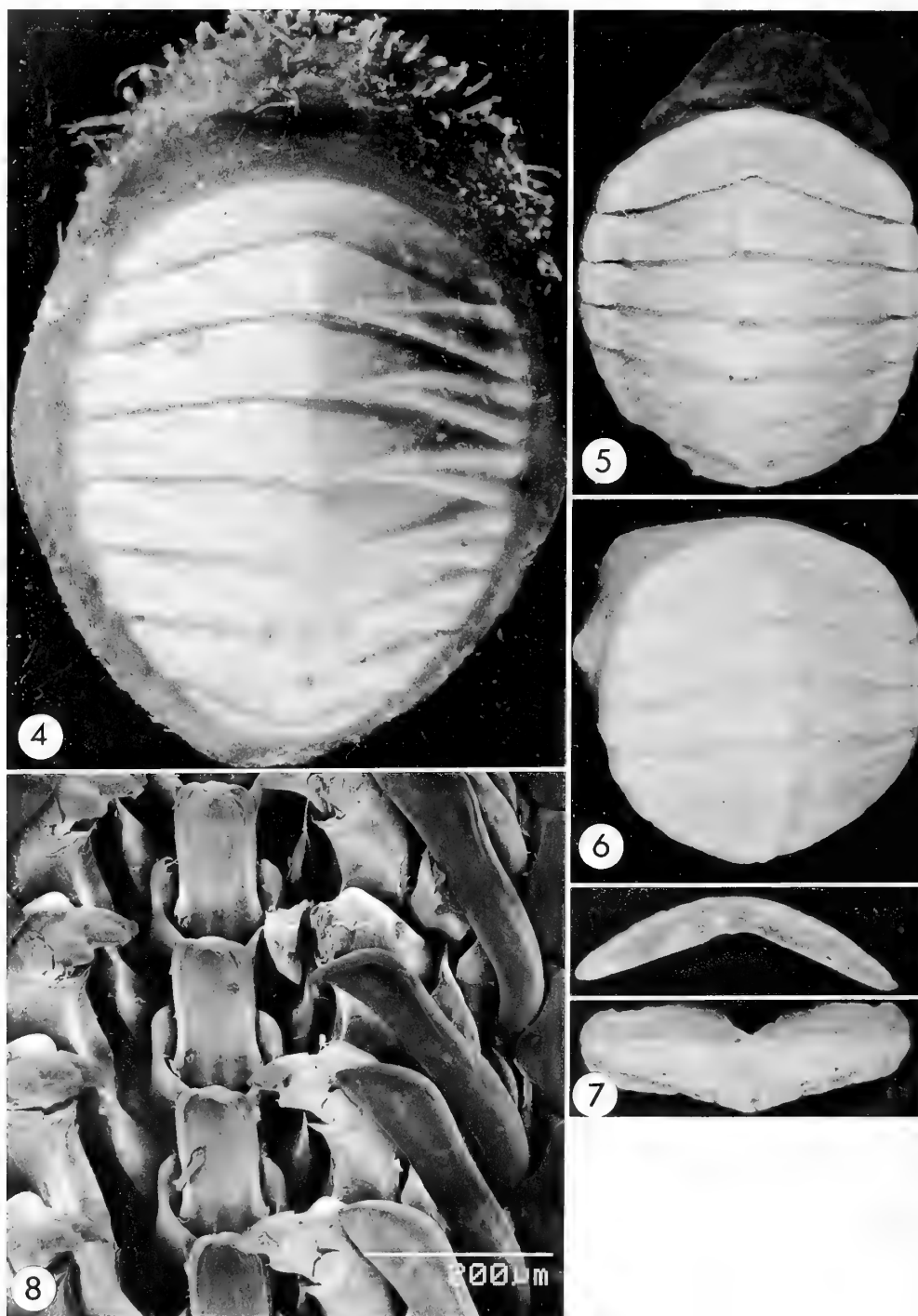
Placiphorella pacifica Berry, 1919:6; Dall, 1921:197; Oldroyd, 1927:314 [916]; Smith & Hanna, 1952:389, pl. 20, figs. 6, 10, 11; Bernard, 1967:8; Burghardt & Burghardt, 1969:33; Abbott, 1974:403; Talmadge, 1973:232; Smith, 1975:159, figs. 1–4; Burghardt, 1979:11; Kaas & Van Belle, 1980:94; Putman, 1980:131; Clark, 1982: 152; Clark, 1983a:11; Skoglund, 1989:86; Jones, 1989: 12; Clark, 1991:95.

Placiphorella uschakovii Yakovleva, 1952:76, text fig. 37, pl. 6, figs. 1a–c; Taki, 1962:34; Burghardt, 1979:11; Saito & Okutani, 1989:209.

Placiphorella albitestae Taki, 1954:22, pl. 11–15; Taki, 1962: 34; Burghardt, 1979:11; Kaas & Van Belle, 1980:5; Wu & Okutani, 1985:123, figs. 1–8, pl. 1; Kaas, 1985:314; Saito & Okutani, 1989:209.

Placiphorella atlantica (Verrill & Smith), Smith, 1960:162, fig. 40:5; Abbott, 1974:403, fig. 4741; Kaas, 1979:13; Kaas & Van Belle, 1980:12; Snell, 1992:143, figs. 1–3.

Placiphorella stimpsoni (Gould), Wu & Okutani, 1985:126, figs. 9–18. *Non Chiton stimpsoni* Gould, 1859.



Explanation of Figures 4 to 8

Placiphorella atlantica (Verrill & Smith, 1882).

Figure 4. Whole animal, RNC 627. Attu Island, Aleutian Islands, Alaska, 408 m. 19.0 mm × 14.5 mm.

Figure 5. Holotype, USNM 106921. Martha's Vinyard, Massachusetts, 1170 m. approx. 19.0 mm in length.

Figure 6. Paratype of *Placiphorella uschakovi* Yakovleva, 1952.

CAS 019464. Sakhalin Island, Sea of Okhotsk, Russia, 500 m. approx. 20.0 mm in length.

Figure 7. Lectotype of *Placiphorella pacifica* Berry, 1919, SBMNH 34394. Kasaan Bay, Prince of Wales Island, Alaska, 179 m. Intermediate valve, 1.0 cm in width.

Figure 8. Radula, RNC 627. Attu Island, Aleutian Islands, Alaska, 408 m.

Diagnosis: Chitons of medium size (up to 3.6 cm), broadly oval in outline, valves uniform milky white in color. Girdle sparsely covered with spinose setae, especially at the periphery, often bare, except at the periphery. Rachidian tooth of radula rectangular, about 160 μm in length and 85 μm in width, with a small cusp at the center of the working edge.

Description: Body (Figure 4) broadly oval in outline; valves depressed, subcarinate, side slopes straight, surface of tegmentum microgranular, uniform milky white in color. Girdle broadly expanded anteriorly, sparsely covered with spinose setae (often missing except at margin), uniform cream to light brown in color. Lectotype (Figure 5) 19.0 mm \times 15.0 mm \times 5.0 mm. Largest specimen examined (RNC 184b) 36.0 mm \times 25.5 mm \times 6.0 mm (N of Umnak Island, Aleutian Islands, Bering Sea, Alaska).

Valves: Head valve crescent-shaped, anterior slope concave, posterior margin not raised; tegmentum with 10–20 radiating grooves; interior smooth, thickened anteriorly; insertion teeth short, rarely extending beyond eaves, relatively thick, anteriorly rugose, with 8–20 slits; slit rays obsolete.

Intermediate valves oblong in outline, very wide and short, widest at valve iv, subcarinate, weakly beaked posteriorly, slightly false-beaked in older specimens; lateral areas raised and cut by a wide sulcus into two low ribs; central areas smooth except for growth lines; interior smooth, with transverse callus running from center to near slits; slit rays obsolete; sutural laminae very large and thick, nearly straight, sharp at anterior edge, separated by a jugal sinus; insertion teeth extending well beyond eaves.

Tail valve small, depressed; mucro posterior and raised; anterior area smooth except for growth lines; posterior area thickened, posterior margin indented; sutural laminae broad, truncated anteriorly, separated by a rather narrow sinus; insertion teeth very short (often obsolete) and thick; interior with thick posterior callus; normally with one slit per side, but range from 0–2, separated by a shallow sinus.

Girdle: Narrow posteriorly, becoming broadly extended anteriorly, covered with minute, weakly striated spicules 50–55 μm in length; margin of girdle with short, spinose series of setae up to 0.5 mm in length, and posterior to this series one to two longer series of setae (Figure 28) about 2 mm in length, with tightly packed spicules. Similar setae scattered about surface of "head flap," but usually broken off. Spicules of setae (Figure 29) sharply pointed distally, about 25 μm in length and 3.5 μm in width; margin of girdle fringed with blunt, very weakly striated spicules about 75 μm in length; hyponotum (except for head flap) clothed with minute spicules about 25 μm in length; head flap with minute papillae and sparsely scattered spicules.

Pallial fold well developed, incised posteriorly, modified anteriorly into 7–10 precephalic tentacles. Gills nearly holobranchial, extending from under suture of valves ii and iii to valves vii; about 20–24 plumes per side in specimens over 20 mm in length.

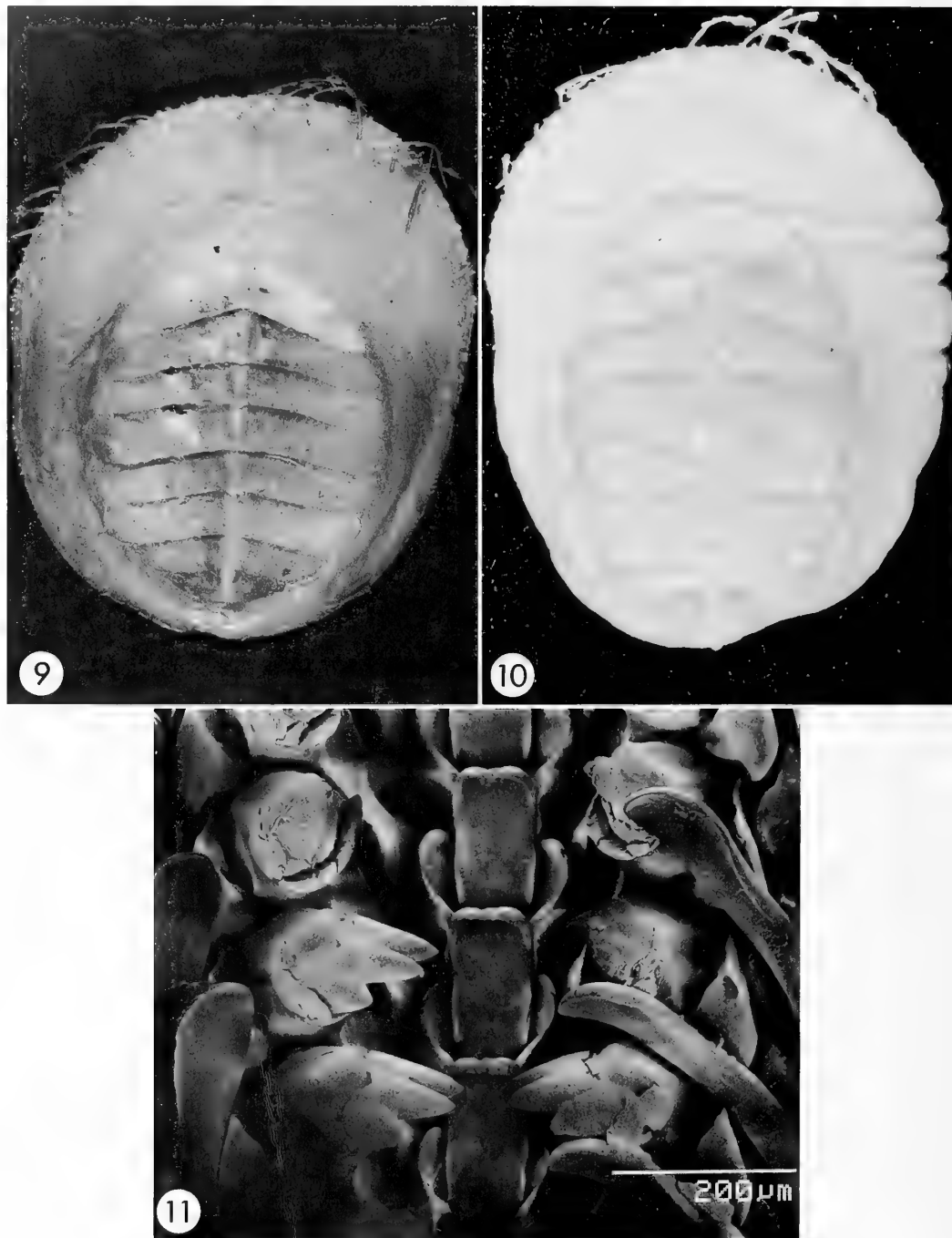
Radula (Figure 8): 5 mm in length (in specimen 20 mm long [RNC 184a]) with about 30 rows of mature teeth; rachidian tooth 160 μm in length, working edge about 85 μm in width, spatulate uncinals very large, about 300 μm in length and 60–65 μm in width at distal end; outer edge thickened and rounded distally, inner edge nearly straight, forming a sharp angled corner where they meet.

Type locality: Off Nantucket Island, Massachusetts (40°01'N, 68°54'W), 1170 m.

Type material: Holotype, USNM 106921; holotype of *P. uschakovi*, ZIAS; paratype of *P. uschakovi*, CAS 019464, N of Cape Elizabeth, Sakhalin Island, Sea of Okhotsk, Russia, 500 m; lectotype of *P. pacifica*, SBMNH 34394, Kasaan Bay, Prince of Wales Island, SE Alaska, 173–179 m.

Additional material: RUSSIA: 1, CAS 014381, NE Sea of Okhotsk, 420 m; 2, SBMNH 35135, off Cape Rollin, Simurshir Island, Kurile Islands, 416 m. ALASKA: 9, RNC 184, N of Umnak Island, Aleutian Islands, 228–274 m; 2, RNC 627, Attu Island, Aleutian Islands, 408 m; 1, RNC 689, Gulf of Alaska, W of Prince of Wales Island, 461 m; 1, Cowan Collection RBCM, near Prince of Wales Island, 205 m. BRITISH COLUMBIA, CANADA: 1, LACM 25177, off Queen Charlotte Islands, 1280 m; 1, Cowan Collection, RBCM, WNW of Triangle Island, 860–878 m; 1, Cowan Collection RBCM, off N end of Vancouver Island, 155 m. OREGON: 3, Cowan Collection RBCM, off Lincoln County; 1, CAS 014379, off Coos County, 1000 m. CALIFORNIA: 1, CAS 014375, off Cordell Bank, Marin County, 365–730 m; 2, CAS type series 561, 562, Pioneer Seamount, off San Mateo County, 914–1189 m; 1, LACM 10543, Monterey Submarine Canyon, Monterey Bay, 500 m; 1, CAS 014301, NW of Point Pinos, Monterey County, 366 m. MEXICO: USNM 206614 off Guaymas, Sonora (depth not stated). CHILE: 1, CAS uncatalogued, off Soutar, 420–450 m. SOUTH PACIFIC OCEAN: 1, LACM 34412, SW of Auckland Islands, New Zealand (51°07'S, 162°02'E), 1647–1665 m; 1, LACM 118723, N of Macquarie Island, Australia (54°32'S, 159°02'E), 494–714 m; 2, LACM uncatalogued, South Tasmanian Rise (42°21'S, 147°51'E), 910–915 m; 2, RMNH K5066, Makassar Strait, Indonesia (00°02'S, 119°50'E), 411–445 m. FRANCE: 1, RMNH K4753, Bay of Biscay (47°40.9'N, 08°5.7'W), 1174 m.

Distribution: Cosmopolitan, bathyal-abyssal. *Placiphorella atlantica* is one of only two species of chitons (the other is *Leptochiton alveolus* [Lovén, 1846, ex Sars MS]) known to be distributed throughout the world's oceans, having been collected off the Atlantic coast of North America from near Maine (Pilsbry, 1893) to off Florida (B. Sirenko, personal communication, 1992); off Europe and Africa between latitudes 25°N and 62°N (P. Kaas, personal communication, 1992); off the Pacific coast of North America from the Bering Sea to the Gulf of California; off South America near Chile; off Asia from the Sea of Okhotsk to



Explanation of Figures 9 to 11

Placiphorella rufa Berry, 1917.

Figure 9. Whole animal, RNC 413. Mountain Point, 8 km S of Ketchikan, Revillagigedo Island, Alaska, 25–30 m. 35.0 mm × 30.0 mm.

Figure 10. Holotype. SBMNH 34373. Forrester Island, Alaska, 46 m. 32.0 mm × 26.0 mm.

Figure 11. Radula (RNC 413).

the Makassar Strait, Indonesia; near Australia, Tasmania, and New Zealand; and in Antarctic seas.

Habitat: Found at depths of 155 to 1665 m on rocks and boulders, or in the case of very small juveniles (<9 mm)

in the Aleutian Islands, on the giant bathyal-abyssal barnacle *Balanus evermani*, sometimes near an unidentified, thin, light tan to yellow encrusting sponge.

Remarks: Comparison of the holotype of *Placiphorella at-*

lantica (Figure 5) with several specimens of *P. pacifica* from throughout the Pacific demonstrated their conspecificity. Authors since Pilsbry (1893) have placed this species in the subgenus *Placophoropsis* Pilsbry, 1893, based on the lack of slits in the tail valve of the holotype. However, this is an aberrant character, as the number of slits in the tail valve of most species of *Placiphorella* varies with age. Berry (1919) did not designate a type in his original description, and the specimen has subsequently been designated as a lectotype by Scott et al. (1990:8).

Placiphorella rufa Berry, 1917

(Figures 9–11, 30, 31)

Placiphorella rufa Berry, 1917a:232, figs. 3–4; Dall, 1921:127; Oldroyd, 1927:316 [918]; Burghardt & Burghardt, 1969:34, pl. 4, fig. 69; Abbott, 1974:403; Burghardt, 1979:11; Putman, 1980:134, fig. 68; Kaas & Van Belle, 1980:114; Clark, 1982:152; Clark, 1983a:11; Baxter, 1987:106; Clark, 1991:95; Anderson, 1992:205 (fig. only).

Placiphorella borealis Pilsbry, Vermeij et al., 1990:349. *Non P. borealis* Pilsbry, 1893.

Diagnosis: Chitons of medium size (to 5.0 cm), broadly oval; valves uniform reddish in color. Girdle nude except at periphery, which bears two series of long, slender setae. Rachidian tooth of radula rectangular, about 160 μ m in length and 90–95 μ m in width, bearing very slight indentation at center of distal end.

Description: Body (Figure 9) broadly oval in outline; valves depressed, subcarinate, side slopes nearly straight to convex; tegmentum microgranular, uniform reddish in color (central portion of head valve paler). Girdle broadly extended anteriorly, uniformly cream or mottled cream and green in color, nude except at margin which bears four series of setae, the inner two series fairly long (up to 5.0 mm), slender, reddish-brown in color. Holotype (Figure 10) 32.8 mm \times 26.0 mm \times 6.0 mm. Largest specimen examined (RNC 1126) 55.0 mm \times 46.0 mm \times 8.5 mm (Ketchikan, Revillagigedo Island, Alaska).

Valves: Head valve crescent-shaped, anterior slope concave, posterior margin raised, apical notch small; tegmentum with 8–11 faint radial grooves; interior smooth, thickened anteriorly; insertion teeth short, thick, pectinate, with 7–10 (normally eight) slits; slit rays obsolete.

Intermediate valves oblong in outline, very wide and short, widest at valve iv, sub-carinate, slightly beaked posteriorly, false-beaked anteriorly; lateral areas raised, flattened; central areas smooth except for growth lines; interior smooth, with transverse callus running from center to near slits; slit rays obsolete; sutural laminae very large and thick, nearly straight, sharp at anterior edge, separated by a sinus, not usually connected across the jugum; insertion teeth long for genus, extending far beyond narrow eaves; one slit per side.

Tail valve small, roughly rhombic, width including articulation nearly three-fourths the width of valve iv

tegumentum; anterior margin convex, anterior area smooth except for growth lines; mucro at posterior one-third; posterior margin straight or very weakly indented; lateral ribs raised, posterior area slightly swollen; sutural laminae very broad, truncated anteriorly, separated by rather narrow sinus; insertion teeth very short; with one slit per side separated by shallow caudal sinus.

Girdle: Nude dorsally except at margin, which bears four series of setae, the outer two series very short (<0.5 mm) and spinose; inner two series (Figure 30) fairly long (up to 9.0 mm), with tightly packed, long, smooth scales tapering to a point proximally, and bluntly rounded distally (Figure 31), about 250 μ m in length. Hyponotum nude; margin of girdle fringed with minute, pointed spicules, 50–125 μ m in length.

Pallial fold well developed, incised posteriorly, modified anteriorly into 12–15 tentacles, the longest at center, becoming gradually shorter toward the edges. Gills merobranchial, extending from under valve ii to the suture of valves vi and vii; about 19–22 plumes per side.

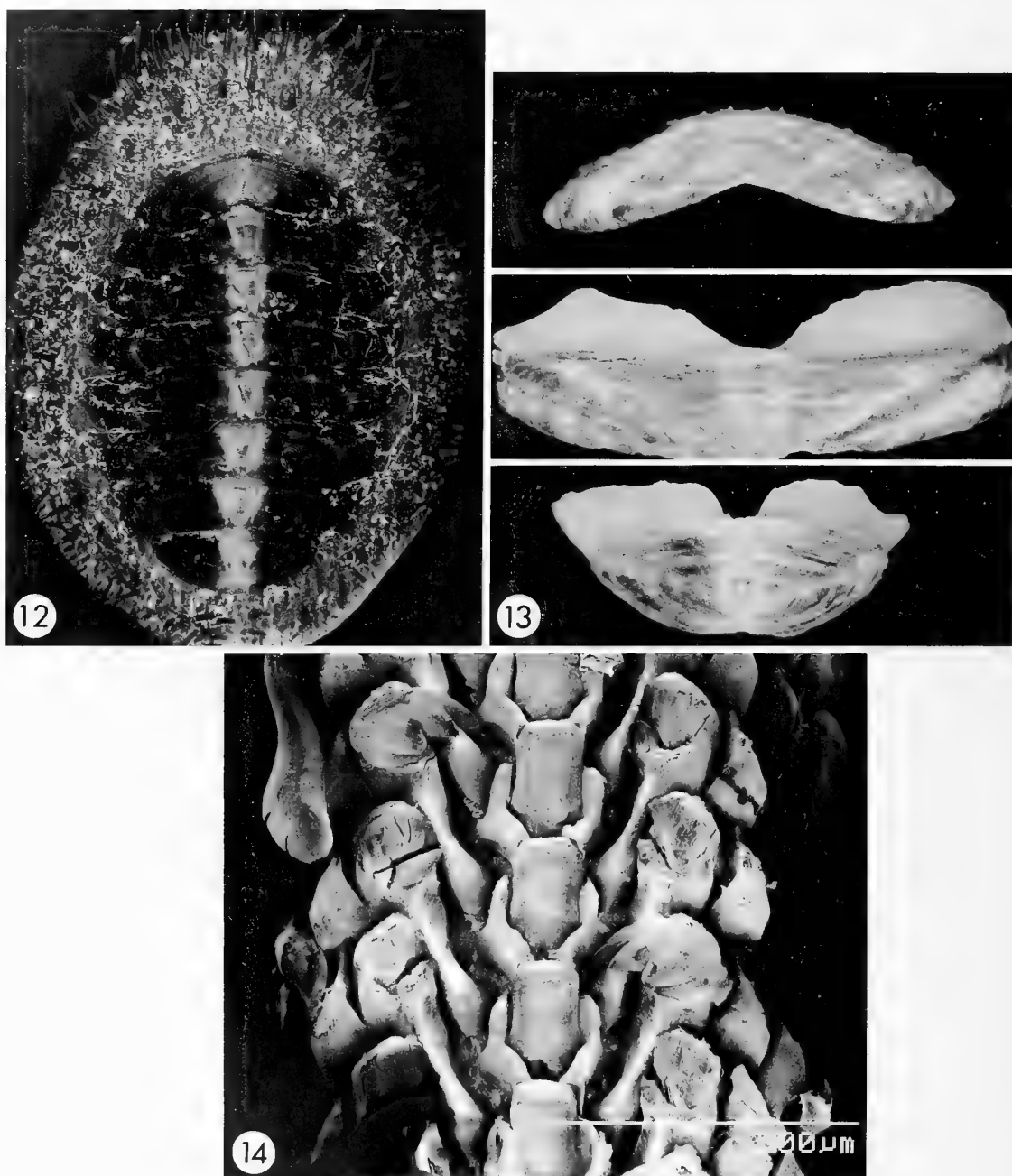
Radula (Figure 11): 11.0 mm long (in specimen 36 mm long [RNC 903]) with about 40 rows of mature teeth; rachidian tooth rectangular, about 160 μ m in length, working edge about 90–95 μ m wide; spatulate uncinial teeth about 375 μ m in length, flattened, thickened along outside edge, distally rounded, about 40 μ m in width at base, broadening to about 75 μ m at distal end.

Type locality: Forrester Island, SE Alaska (54°50'N, 133°30'W), 27–36 m.

Type material: Holotype, SBMNH 34373; Paratypes, 3, SBMNH 34374; 1, SBMNH 34375; 1, SBMNH 34376; 1, CAS 066404.

Additional material: ALASKA: 1, UCD uncatalogued, Adak Island, Aleutian Islands, 3–5 m; 1, UAF Collection Spruce Island; 1, RNC 328, Deep Bay, Hawkins Island, 30–35 m; 1, CAS 014377, Prince William Sound; 1, RNC 421, Hesketh Island, Kachemak Bay, 0–1 m; 1, RNC 24, Kachemak Bay, 0–1 m; 1, CAS 014372, Auke Bay, 18 m; 2, CAS 014410, Gambier Bay, Admiralty Island, 18 m; 1, NMFAB AB82-30, Burnett Island, 3–15 m; 2, NMFAB AB82-35, Pybus Bay, Elliot Island, 24 m; 2, RNC 127, Sitka, Barenof Island, 1 m; 13, RNC 1133, Eastern Sukoi Island, 10–15 m; 29, RNC 1126, RNC 903, near Ketchikan, Revillagigedo Island, 3–30 m; 7, RNC 906, Petersburg, Mitkof Island, 1–2 m; 1, RNC 658, Metlakatla, Annette Island, 43 m. BRITISH COLUMBIA, CANADA: 6, RBCM 976-1064-5, Sonora Island; 1, RBCM 976-1046-2, Edward King Island, Barkley Sound. OREGON: 1, LACM 19336; 1, RNC 962, Island Rock, Curry County, 30 m. Seventeen additional lots examined.

Distribution: Central Aleutian Islands to southern Oregon. Westernmost record Lucky Point, SW shore Kuluk Bay, Adak Islands, Aleutian Islands, Alaska (51°51'20"N, 176°35'W) 5–7 m (Vermeij Collection, UCD); northernmost record Deep Bay, Hawkins Island, Prince William



Explanation of Figures 12 to 14

Placiphorella borealis Pilsbry, 1892.

Figure 12. Whole animal, RNC 947. Bering Island, Commander Islands, Russia, 0-1 m. 34.0 mm × 25.0 mm.

Figure 13. Holotype, USNM 106922. Bering Island, Commander Islands, Russia. intermediate valve: 25.0 mm in width.

Figure 14. Radula, RNC 192. Atka Island, Aleutian Islands, Alaska, 2 m.

Sound, Alaska (60°40'N, 145°32'W), 30-35 m (RNC 328); southernmost record off Island Rock, Curry County, Oregon (42°40.08'N, 124°28.48'W), 30 m (LACM 19336, RNC 962).

Habitat: *Placiphorella rufa* is usually found on the sides and tops of boulders and on vertical rock walls, generally in areas of moderate to heavy current, from the low intertidal to at least 46 m. It is often observed on rock ledges,

situated perpendicular to the current, with its head flap raised 45°–90°.

Remarks: *Placiphorella rufa* is a relatively common subtidal species which may be readily distinguished from other members of the genus by the uniform reddish coloration of the valves and by the mostly nude girdle, which bears setae only at the periphery.

The setae of *P. rufa* are host to several species of foraminiferans and two or more unknown species of Hydrozoa, probably of the families Lafoeidae and Campanularidae.

The girdle of *P. rufa* is often mottled with green, particularly in older specimens, probably due to the presence of symbiotic algae. This warrants further investigation.

Placiphorella borealis Pilsbry, 1893

(Figures 12–14, 32, 33)

Placiphorella stimpsoni (Gould) Dall, 1886:210 (in part). *Non Chiton stimpsoni* Gould, 1859.

Placiphorella borealis Pilsbry, 1893:309, pl. 66, figs. 14–17; Dall, 1921:196; Oldroyd, 1927:314; Smith, 1947:19; Yakovleva, 1952:75, figs. 3a–c; Taki, 1962:34; Sirenko, 1973:1569; Sirenko, 1979:200; Burghardt, 1979:11; Kaas & Van Belle, 1980:18; Clark, 1982:152; Clark, 1983a:11; Sirenko & Scarlato, 1983:5; Sirenko, 1985:357; Saito & Okutani, 1989:209, figs. 1–10, 47–48; Clark, 1991:95.

Placiphorella sp. O'Clair, 1977:444.

Diagnosis: Chitons of medium size (to 4.0 cm); oval in outline; valves uniform brown to dark brown in color, with pale jugal stipe. Girdle covered with brown setae of several sizes; scales of setae broad, roughly diamond-shaped, striated along distal half, and mammillated at distal end. Rachidian tooth of radula subrectangular, 180 μ m in length and 120 μ m in width at working edge; posterior third tapering sharply to about 50 μ m at the base.

Description: Body (Figure 12) oval in outline; valves depressed, subcarinate, side slopes nearly straight; tegmentum microgranular, dark brown with cream to white jugal stripe. Girdle broadly extended anteriorly, densely covered with short brown setae of various sizes. Holotype disarticulated (Figure 13); largest specimen examined (RNC 192b, Atka Island, Alaska) 41.0 mm \times 30.5 mm \times 5.0 mm.

Valves: Head valve thick, crescent-shaped, anterior slope concave to nearly straight, posterior margin thick, convex, apical notch small, round; tegmentum with six to 10 very low, faint (often obsolete), radiating ribs, and concentric growth lines; interior smooth, thickened anteriorly; insertion teeth short, thick, slightly pectinate, with seven to 10 (normally eight) slits; slit rays obsolete.

Intermediate valves oblong in outline, very wide and short, widest at valve iv, beaked posteriorly in young specimens (<20 mm), becoming unbeaked in adults, slightly false-beaked anteriorly; lateral areas raised, separated into two ribs by a broad groove; central areas unsculptured

except for growth lines; interior smooth, with transverse callus running from center to near slits; with one slit per side, slit rays weakly grooved in young, obsolete in adults; sutural laminae very large and thick, separated by fairly wide jugal sinus, not connected across jugum; insertion teeth long for genus, extending far beyond narrow eaves, upswept (as are sutural laminae) at sides of slits.

Tail valve large for genus, depressed, nearly oval in outline, more than half the width of valve iv tegmentum; anterior margin convex and elevated, mucro at posterior third, slightly raised; anterior area sculptureless except for growth lines, diagonal rib broad and convex; posterior area strongly sloping; posterior margin weakly indented; interior calloused posteriorly; sutural laminae broad, truncated anteriorly, separated by a sinus; insertion teeth very short and thick, with one slit per side.

Girdle: Perinotum densely covered with minute, pointed spicules, about 30–45 μ m in length, and large (up to 4 mm) brown, scaled bristles (Figure 32) of several sizes and series, the largest at about midpoint of girdle, five to seven in front of anterior valve, one adjacent to each valve suture, and three behind posterior valve; similar series at anterior margin of girdle, from about valve ii forward; other bristles of various sizes, scattered; scales of bristles (Figure 33) about 100–120 μ m in length; striated on distal half, and bearing short spicule. Hyponotum sparsely covered from suture of valves i and ii to anal cleft with smooth, blunt-tipped spicules about 50–60 μ m in length; anterior portion of hyponotum with numerous small papillae; margin of girdle fringed with slender, blunt-tipped spicules about 100–150 μ m in length.

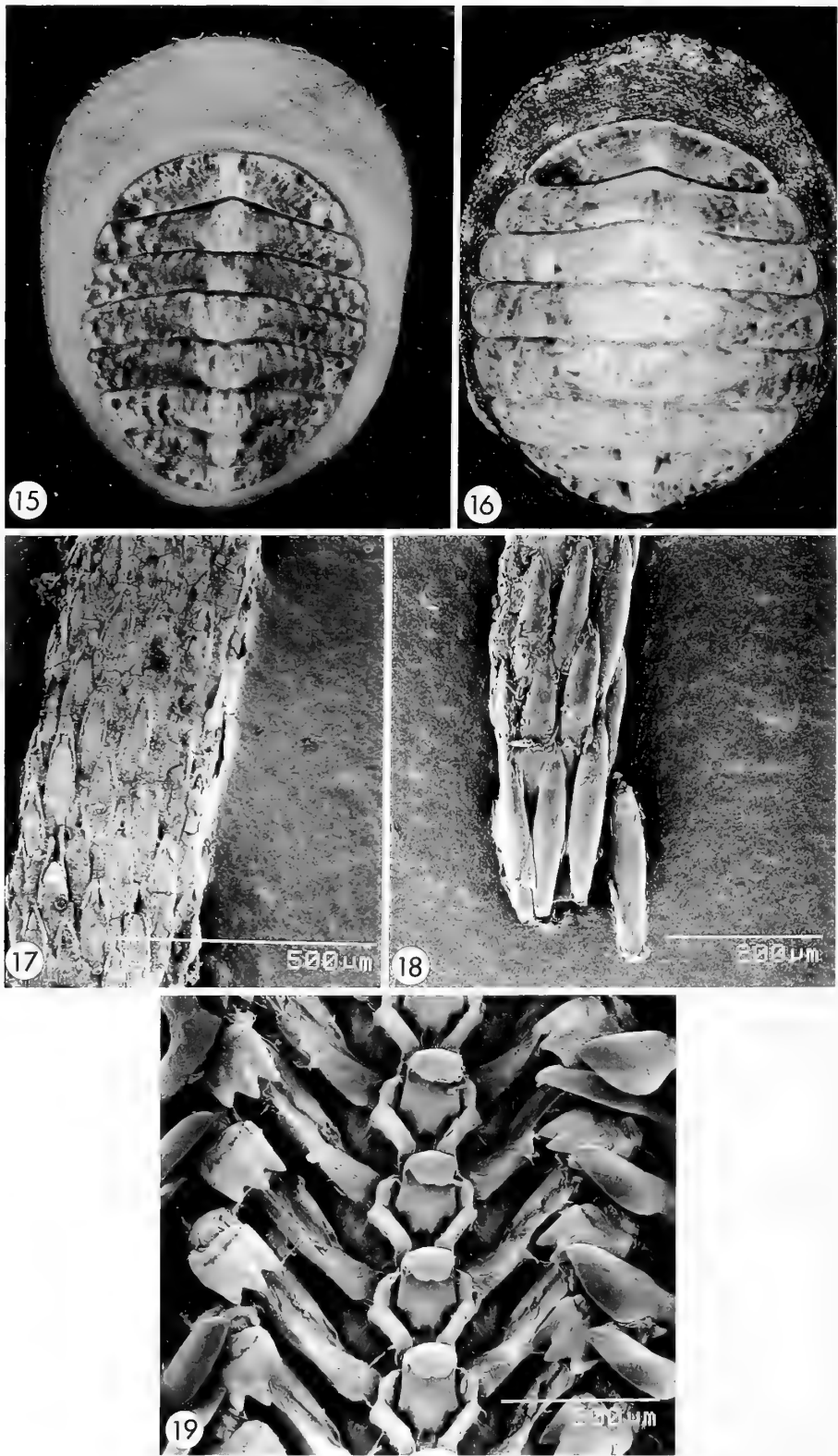
Pallial fold well developed, incised posteriorly, modified anteriorly into 15–24 precephalic tentacles. Gills holobranchial, extending from suture of valves ii and iii to suture of valves vi and vii; 17–21 plumes per side.

Radula (Figure 14): Approximately 7.5 mm long (fragmented) in specimen 26.0 mm long (RNC 192b, Atka Island, Alaska), with approximately 33 rows of mature teeth. Rachidian tooth subrectangular, 180 μ m in length, working edge 120 μ m in width, posterior third tapering sharply to about 45–50 μ m in width at base. Spatulate uncinals about 450 μ m in length, very broad distally (about 120 μ m), tapering to about 50 μ m at base.

Type locality: Bering Island, Commander Islands, Bering Sea, Russia (55°00'N, 165°15'E).

Type material: Holotype, USNM 106922.

Additional material: JAPAN: 1, RNC 493, Nosappu, Hokkaido Island. RUSSIA: 1, CAS 014380, Petrova Island, Sea of Japan, 0–1 m; 1, RNC 119, Zelenij Island (Green Island), Kurile Islands, 13 m; 1, RNC 869, Iturup Island, Kurile Islands, 5 m; 1, RNC 733, Paramushir Island, Kurile Islands; 3, CAS 014373, Bering Island, Commander Islands; 2, RNC 947, Bering Islands, Commander Islands; 2, RNC 126, Mendji Island, Commander Islands.



ALASKA: 1, LACM 141155; 3, RNC 192, Atka Island, Aleutian Islands, 1–2 m and 12–18 m.

Distribution: *Placiphorella borealis* is distributed throughout the northwestern Pacific island arc, from SE Hokkaido Island, Japan (41°57'N, 143°15'E), to Atka Island, Aleutian Islands, Alaska (52°54'N, 174°18'W).

Habitat: *Placiphorella borealis* is found on the bottoms of cobbles and boulders or in crevices in rock walls, from the low intertidal to about 24 m.

Remarks: *Placiphorella borealis* was long considered to be a deep-water species, based on Berry (1917b), who described and illustrated specimens of what he interpreted as this species taken at 416 m off Simushir Island, Kurile Islands, Russia, by the *Albatross* expedition in 1906. However re-examination of these specimens has revealed them instead to be *P. atlantica* (Clark, 1991:95).

Sirenko (1973) reported that *P. borealis* broods its young in the pallial grooves. This is the only member of Mopaliidae known to exhibit this behavior. The date of description of *P. borealis* has been cited by some authors as 1892. However, the section of the *Manual of Conchology* that contained the description of *P. borealis* was published in 1893 (see Clench & Turner, 1962).

Placiphorella blainvillii (Broderip, 1832)

(Figures 15–19)

Chiton blainvillii Broderip, 1832:27; Sowerby, 1833:pl. 38, fig. 6; Reeve, 1847:3, fig. 13.

Mopalia blainvillii (Broderip), Gray, 1847:69; Dall, 1879:303.

Placiphorella blainvillii (Broderip), Dall, 1886:210; Pilsbry, 1893:310, pl. 66, figs. 26–32; Dall, 1908:357; Dall, 1909:246; Smith, 1960:162, fig. 40:4; Hertlein, 1963:243; Thorpe (in Keen), 1971:882, fig. 49; Smith & Ferreira, 1977:88, fig. 12; Burghardt, 1979:11; Ferreira, 1987:46; Shasky, 1989:75, fig. 4; Skoglund, 1989:86.

Diagnosis: Chitons of medium size (to 5 cm), oval to broadly oval in outline; valves white variegated with light brown, olive, and reddish brown, often suffused with pink, especially along the center. Girdle sparsely covered with short setae; scales of setae smooth, cylindrical, and pointed at the distal end. Rachidian tooth of radula angular, pos-

terior third sharply truncated and forming three sharp denticles (very small central, and two large lateral) at base.

Description: Body (Figure 15) broadly oval in outline, valves moderately elevated, subcarinate, side slopes straight; tegmentum microgranular, white variegated with light brown and olive or reddish brown, often suffused with pink, especially along the center. Girdle broadly extended anteriorly, sparsely covered with rather fine, short setae; uniform light tan to brown in color. Lectotype (largest specimen examined) 48 mm × 36 mm × 10.5 mm.

Valves: Head valve thick, crescent-shaped, anterior slope nearly straight to convex, apical notch small, round; tegmentum sculptureless except for growth lines; interior smooth, thickened anteriorly; insertion teeth short and smooth, not pectinate; with 10 to 13 slits; slit rays obsolete.

Intermediate valves oblong in outline, wide and short, widest at valve iv; beaked posteriorly, slightly false-beaked anteriorly; lateral areas raised and smooth; central areas lacking sculpture except for growth lines; interior smooth, with transverse callus extending from center to near slits; sutural laminae wide and rather short; straight and sharp at anterior edge, connected across jugum; insertion teeth short, smooth, with one slit per side.

Tail valve small, width less than half the width of valve v tegmentum; anterior margin sharply convex; anterior area convex, lacking sculpture except for growth lines; mucro terminal; lateral ribs raised, thick, smooth, sloping sharply to posterior margin of valve. Interior smooth, with posterior callus; sutural laminae long and sharp, not connected across jugum; insertion teeth very short and blunt; one slit per side separated by shallow caudal sinus.

Girdle: Perinotum sparsely covered with short, pointed spicules about 150 μ m in length, occurring singly or in groups of two or three, and short (1–1.5 mm) yellow-brown setae (Figures 17, 18), in three series at periphery of girdle, one in valve sutures, others sparsely scattered; scales of marginal series smooth, cylindrical, pointed, about 260 μ m in length and 45 μ m in width; scales of sutural and scattered dorsal series similar to those of marginal series but shorter and proportionally broader, about 190–200 μ m in length and 50 μ m in width. Hyponotum from posterior edge of head valve to anal cleft carpeted with overlapping, outwardly directed, minute, pointed scales, about 75–80 μ m in length and 25–30 μ m in width; anterior portion of

Explanation of Figures 15 to 19

Placiphorella blainvillei (Broderip, 1832).

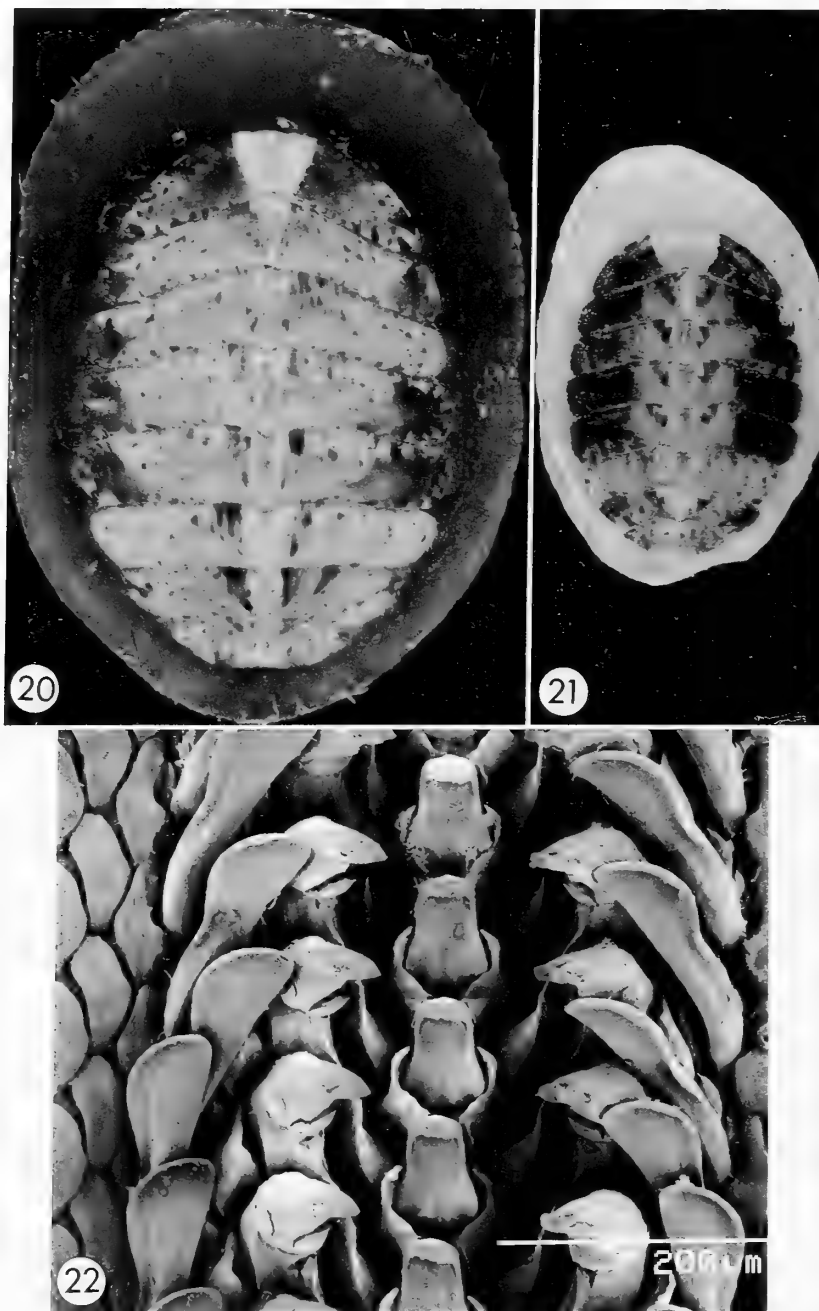
Figure 15. Whole animal, ANSP A13339. Cocos Island, Costa Rica, 80–88 m. 40.0 mm × 31.0 mm.

Figure 16. Paralectotype, BMNH 1967618/3. Lobos de Tierra, Peru, 31 m. 35.5 mm × 28.0 mm.

Figure 17. Dorsal setae, LACM 38–39.4. Cocos Island, Costa Rica, 73–84 m.

Figure 18. Marginal setae, BMNH 1967618/3.

Figure 19. Radula (LACM 38–39.4).



Explanation of Figures 20 to 22

Placiphorella mirabilis Clark, sp. nov.

Figure 20. Whole animal, Paratype, RNC 1079. San Nicholas Island, California, 30 m. 24.5 mm × 18.0 mm.

Figure 21. Holotype, LACM 2703. Catalina Island, California, 69 m. 15.25 mm × 10.1 mm.

Figure 22. Radula, Paratype, LACM 2704. Catalina Island, 82–91 m.

hyponotum devoid of scales and spicules, bearing only very minute papillae; margin of girdle fringed with sharply pointed spicules, about 180 μm in length.

Pallial fold well developed, incised posteriorly, modified

anteriorly into 10 to 12 precephalic tentacles. Gills holobranchial, 21–22 plumes per side.

Radula (Figure 19): Approximately 8.5 mm along (in specimen approximately 40 mm in length [LACM 38–

39.4)], with about 60 rows of mature teeth; teeth as noted by Thorpe (1971) smaller and more delicate than those of *Placiphorella velata*. Rachidian tooth about 115 μm in length and 65 μm in width, sharply truncated at the proximal third to about 20 μm ; working edge about 55 μm in width. Spatulate uncinat teeth about 300 μm in length, and 25 μm in width at base, exterior convex, interior slightly concave, abruptly dilated at distal half to about 80 μm ; outside margin nearly straight, inside margin sharply rounded laterally, sharply tapering distally to a point where they meet.

Type locality: Lobos de Tierra (inner Lobos Island), Peru (6°30'S, 80°50'W).

Type material: Six syntypes, one (the largest), BMNH 1967618/1, figured by Pilsbry (1893) here designated as the **lectotype**, and the five remaining, BMNH 1967618/2–6, as **paralectotypes**.

Additional material: COSTA RICA: 2, LACM 38–39.4, Cocos Island, depth not stated (Allan Hancock Foundation); 3, USNM 210799, Cocos Island, 120 m; 1, USNM 122968, Cocos Island, 120 m; 1, ANSP A13339, Cocos Island, 80–88 m; 1, D.R. Shasky Collection, Redlands, California, Cocos Island, 137 m. PERU: 2, BMNH (de Burgh Collection, Accession No. 1822).

Distribution: *Placiphorella blainvillii* has been collected only off Peru and Cocos Island, Costa Rica. Smith & Ferreira (1977) included this species in their review of the chiton fauna of the Galapagos Islands, although no specimens of this species have ever actually been recorded from that locality. The verified northernmost record is Cocos Island, Costa Rica (05°34'N, 86°58'W); the southernmost record is the type locality.

Habitat: *Placiphorella blainvillii* has been taken on rocks and dead coral heads.

Remarks: *Placiphorella blainvillii* is morphologically similar to *P. mirabilis*, but may be distinguished by its smooth, cylindrical setae scales, and the shape of the rachidian radular tooth which is sharply truncated at the posterior third, where it forms three sharp denticles (see discussion under *P. mirabilis*).

Placiphorella mirabilis Clark, sp. nov.

(Figures 20–22, 34, 35)

Placiphorella stimpsoni (Gould), Dall, 1921:127 (in part); Burghardt & Burghardt, 1969:36; Putnam, 1980:12, 132 (in part). *Non Chiton stimpsoni* Gould, 1859.

Diagnosis: Small chitons (to 3.0 cm), oval in outline; valves pink, speckled with dark brown and white, and suffused with pale olive or brownish green. Girdle nearly nude, except at periphery and (rarely) in front of head; scales of peripheral setae with latticelike sculpture, bearing a sharp

spicule at distal end. Rachidian tooth of radula nearly trapezoidal in shape, widest at base.

Description: Body (Figure 20) broadly oval in outline, valves subcarinate, side slopes straight to convex, tegmentum microgranular, pink, speckled with dark brown and white, and suffused with green, occasionally with brown or green subjugal triangles; girdle broadly extended anteriorly, uniformly cream to light tan in color. Holotype (Figure 21), 15.25 mm \times 10.1 mm \times 3.0 mm. Largest specimen examined 29.0 mm \times 23.0 mm \times 5.0 mm (C.M. Hertz Collection, San Diego, California).

Valves: Head valve narrowly crescent-shaped, anterior slope straight to slightly convex, with small rounded notch at apex; tegmental surface smooth except for concentric growth lines; anterior margin barely raised; interior smooth, strongly thickened anteriorly; insertion teeth short, thick, and weakly pectinate, with (normally) eight slits, sometimes more due to splitting; slit rays inconspicuous.

Intermediate valves oblong in outline, very wide and short, widest at valve iv, subcarinate, beaked posteriorly, weakly false-beaked anteriorly; lateral areas slightly raised, with obsolete diagonal rib; central areas smooth except for concentric growth lines; interior smooth, with transverse callus extending from center to near slits; slit rays porous and barely perceptible in young, obsolete in adults; sutural laminae very large and thick, nearly straight, sharp at anterior edge, strongly squared at outer edge, especially in valves v–vii, widely incised by jugal sinus, usually slightly connected across jugum; insertion teeth long for genus, usually extending beyond narrow eaves, lateral surface of teeth slightly pectinate, insertion teeth and sutural laminae upswept at sides of slit.

Tail valve small, roughly rhombic, width (including articulation) less than half the width of valve iv; anterior margin convex, without false beak; mucro slightly raised, situated near posterior edge, with moderate caudal sinus; central anterior area smooth, convex; diagonal ribs raised and smooth, posterior area thickened, roughened by growth lines; interior of valve smooth, posteriorly calloused; sutural laminae broad, anterior edge sharp, lateral edge sharply squared, separated by narrow sinus; insertion teeth short but clearly defined, with one slit per side separated by wide sinus.

Girdle: Perinotum mostly nude, bearing three series of scaled bristles: primary series, five large bristles in front of anterior valve (nearly always missing), one each adjacent to valve sutures, at about midpoint of girdle, and three behind posterior valve; long, narrow submarginal series (Figure 34) (up to 3 mm long), with tightly packed scales; and short, thick, very spinose marginal series about 0.5 mm long; scales (Figure 35) measuring about 130 μm in length, and 25 μm in width, tapering distally, and bearing short, broad, pointed spicule at distal end and scattered, minute spicules about 20 μm long, especially on anterior flap. Hyponotum densely covered with minute, outwardly directed spicules, about 10–20 μm long, extending from

about suture of valves ii and iii to anal region; anterior flap almost entirely devoid of spicules, but bearing minute papillae, often coalescing in a vermicular pattern; margin of girdle fringed with narrow spicules (Figure 31) about 100 μ m in length.

Pallial fold well developed; modified anteriorly into 12–14 tentacles (Figure 62), largest at center, becoming smaller toward edges, bearing minute, triangular, pointed scales about 20–30 μ m long. Gills holobranchial, about 15–18 per side, extending from valve ii to valve vii.

Radula (Figure 22): (paratype LACM 2704, 18 mm in length) 4 mm long, with about 37 rows of mature teeth; rachidian tooth nearly trapezoidal, broadly dilated proximally to nearly twice the width of the working edge; spatulate uncinals about 200 μ m in length, broadly rounded distally, to about twice width of proximal end.

Type locality: 1.9 km, 130° T from Long Point, S end of Santa Catalina Island, California (33°23.5'N, 115°13.3'W), 69 m.

Type material: Holotype, LACM 2703 (leg. R. Reimer, B. Banta, G. Bakus, R/V *Velero IV*; 13 February 1965) (Allan Hancock Foundation); 7 paratypes: CALIFORNIA: 1, LACM 2704, E of Long Point, Santa Catalina Island, 82–91 m (leg. R/V *Velero III*, 10 August 1941); 1, LACM 2705, E of White Cove, Santa Catalina Island, 66 m (leg. R/V *Velero IV*, 31 October 1948); 2, LACM 2706, 110° T from Ship Rock, Santa Catalina Island, 82 m (leg. R. Reimer, et al., R/V *Velero IV*; 13 February 1965); 3, RNC 559, SW of Catalina Island, 30–40 m (leg. E. Edmonds, June 1948).

One additional, non-topotypic paratype: RNC 1079, W side of San Nicolas Island, California, 33–35 m (leg. RNC, 15 October 1991).

Additional material: CALIFORNIA: 1, RNC 653, Gaviota, Santa Barbara County; 1, SBMNH 19157, Santa Cruz Island, 78–80 m; 3, CAS 017862, Santa Cruz Island, depth not stated; 1, CAS 01640, Redondo Beach, 46 m; 2, RNC 128, Pyramid Cove, San Clemente Island, 37–41 m on rock; 4, C.M. Hertz Collection nine Mile Bank, off San Diego County, 137 m; 1, LACM 48-43.7, SE of Santa Cruz Island, 42 m; 3, LACM 50-20.3, S of W end of Anacapa Island, 51 m. MEXICO: 2, LACM 71-150.6, SE of Cabo San Quintín, Baja California Norte, 40–55 m; 1, LACM 39-115.1, rock, N end of Ranger Bank (near Isla Cedros), 146–155 m, Baja California Norte; 1, CAS 017465, Cedros Island, Baja California Norte; 1, SBMNH 35630, 22 km off Cabo Colnett, Baja California Norte; depth not stated, 1, SBMNH 35632, tail valve only, Bahía San Bartolomé (Turtle Bay), Baja California Sur; 1, SBMNH 35633, tail valve only, Isla Asunción, Baja California Sur, depth not stated.

Distribution: *Placiphorella mirabilis* has a continuous distribution between Gaviota, Santa Barbara County, Cali-

fornia (34°28'N, 120°14'W) (RNC 653), and Isla Asunción, Baja California Sur, Mexico (27°06'N, 114°18'N).

Habitat: *Placiphorella mirabilis* is found from 28–155 m on large cobbles, boulders, and rock cliffs.

Remarks: At first glance, *Placiphorella mirabilis* appears to be a stunted offshore form of *P. velata* because of the similar coloration of the valves. However, close examination of the placement and structure of the setae reveals it to be a distinct species. *Placiphorella mirabilis* is morphologically similar to *P. atlantica*, *P. blainvillii*, and *P. rufa*, but may be distinguished from these species by the following: (1) setae restricted to periphery of girdle, except for four to five very large setae in front of head valve; (2) peripheral setae very fine and spinose; (3) spicules of setae with latticelike sculpture; (4) trapezoidal shape of rachidian tooth of radula, which is nearly twice as wide at the base as at the working end.

Etymology: The name in Latin means wonderful, suggested by the beautiful coloration of the tegmentum.

Placiphorella hanselmani Clark, sp. nov.

(Figures 23–25, 36, 37)

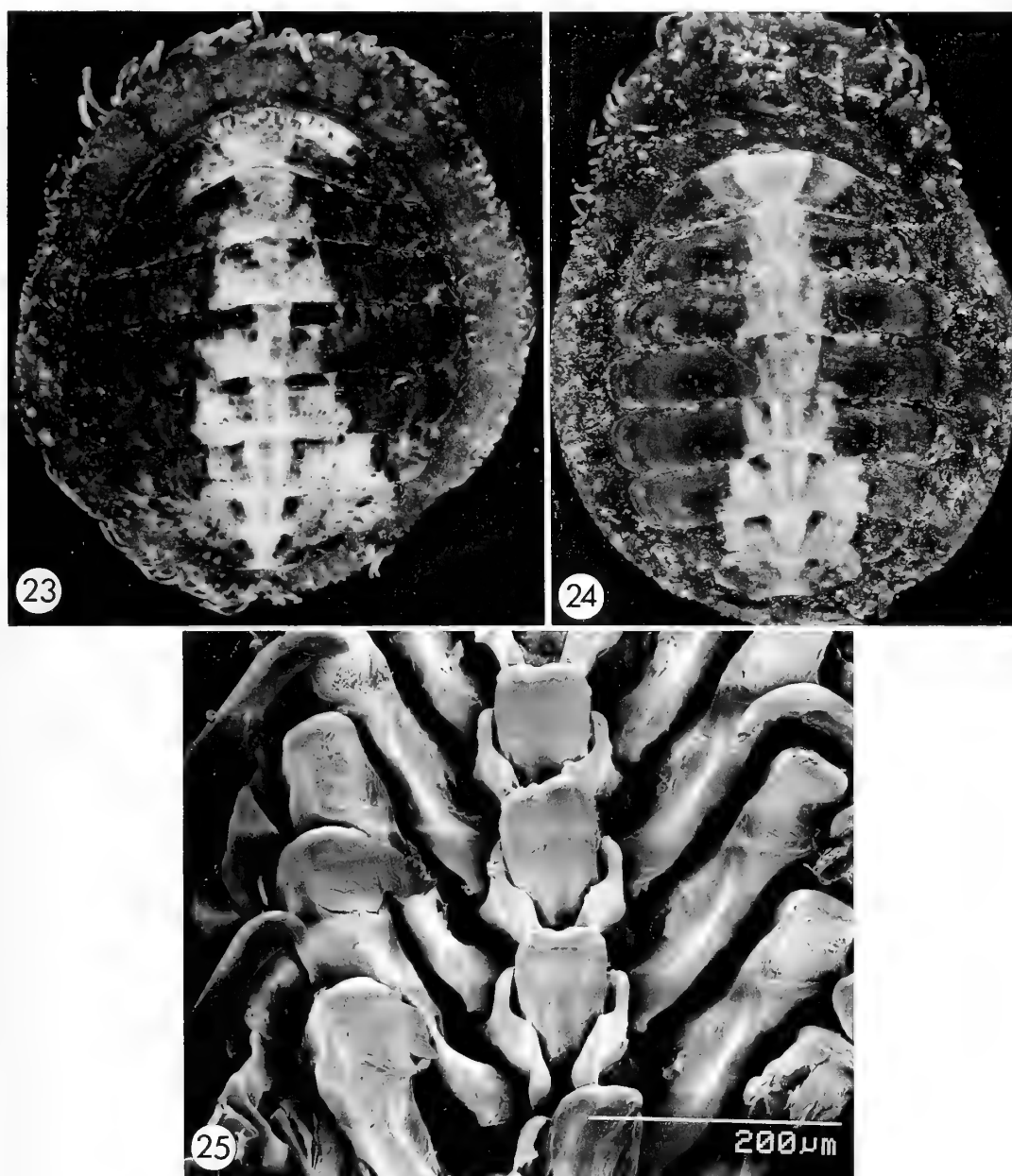
Placiphorella velata Carpenter MS, Dall, Thorpe (in Keen), 1971:882; Skoglund, 1989:86.

Diagnosis: Chitons of medium size (to 3.6 cm), broadly oval in outline; valves buff, speckled with dark brown in the center one-fourth to one-third, remaining portion of valves dark brown. Scales of setae broadly cylindrical, tapering to point proximally, truncated distally, bearing spicule at distal end. Rachidian tooth of radula heart-shaped.

Description: Body (Figure 23) broadly oval in outline; valves depressed, subcarinate, side slopes straight, tegmentum microgranular, color buff, speckled with dark brown on jugal areas and central portion of anterior valve, speckling usually extending to upper fourth or more of pleural areas (especially on valves v–vii), jugal areas bordered with dark brown triangles, remaining portions of valves dark brown. Girdle broadly extended anteriorly, covered with rather short, stiff setae, uniform light brown in color. Holotype (Figure 24) 25.5 mm \times 19.5 mm \times 4.2 mm. Largest specimen examined RNC (512) 36.0 mm \times 29.0 mm \times 9.0 mm.

Valves: Head valve crescent-shaped, anterior slope straight to slightly concave, becoming thickened and somewhat convex in older specimens; posterior margin slightly raised; apical notch small, round; tegmentum sculptureless except for concentric growth lines; interior smooth, thickened anteriorly; insertion teeth short, not extending beyond tegmentum, thick and strongly pectinate (as defined in Saito & Okutani, 1989), with (normally) eight slits; slit rays faint in juveniles, obsolete in adults.

Intermediate valves oblong in outline, very wide and



Explanation of Figures 23 to 25

Placiphorella hanselmani Clark, sp. nov.

Figure 23. Whole animal, Paratype, Hanselman collection, Isla Pata, Bahía de Los Ángeles, Gulf of California, Baja California, Mexico. 22.0 mm × 20.0 mm.

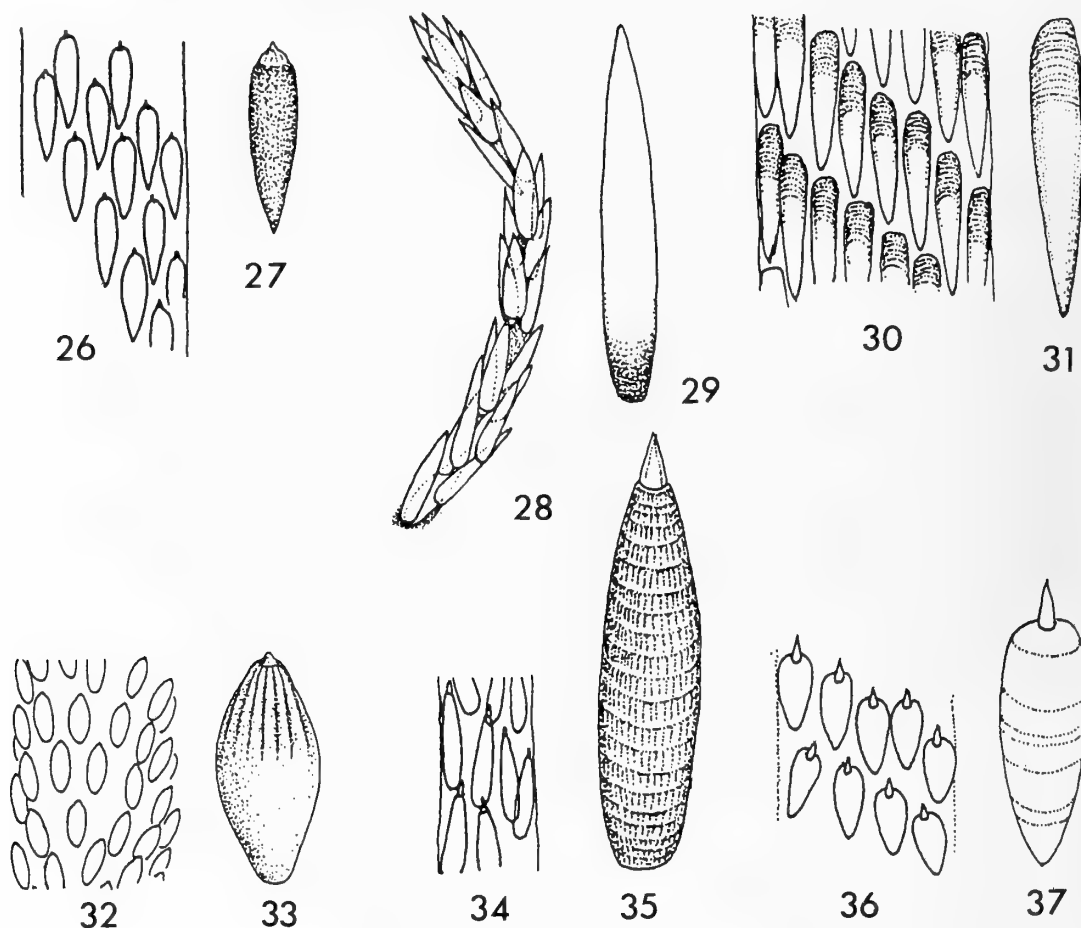
short, widest at valve iv, subcarinate, beaked posteriorly, slightly false-beaked anteriorly; lateral areas raised, flattened, and cut by a shallow sulcus into two low (often obsolete) ribs; central areas nearly smooth except for growth lines; interior smooth, with transverse callus running from center to near slits; slit rays faint and porous in juveniles,

Figure 24. Holotype, LACM 2707. Bahía de Los Ángeles, Gulf of California, Baja California, intertidal.

Figure 25. Radula, Paratype, CAS 075732. Puerto Don Juan, S end of Bahía de Los Angeles, 5 m.

obsolete in adults; sutural laminae very large and thick, nearly straight, sharp at anterior edge, separated by wide jugal sinus, usually connected across jugum; insertion teeth short, not extending beyond eaves, pectinate and upswept at sides of slits, of which there is one (rarely two) per side.

Tail valve small, roughly rhombic, width including ar-



Explanation of Figures 26 to 37

Setae and setae scales/spicules.

Figures 26, 27. *Placiphorella velata* Dall, 1879, ex Carpenter MS. Figure 26, Seta; bar = 0.5 mm. Figure 27, Scale of seta; bar = 0.2 mm.

Figures 28, 29. *Placiphorella atlantica* (Verrill & Smith, 1882). Figure 28, Seta; bar = 1.0 mm. (after Theile, 1910). Figure 29, Spicule of seta; bar = 10 μ m.

Figures 30, 31. *Placiphorella rufa* Berry, 1917. Figure 30, Seta; bar = 0.5 mm. Figure 31, Scale of seta; bar = 250 μ m.

Figures 32, 33. *Placiphorella borealis* Pilsbry, 1892 (after Saito & Okutani, 1989). Figure 32, Seta; bar = 0.5 mm. Figure 33, Scale of seta; bar = 200 μ m.

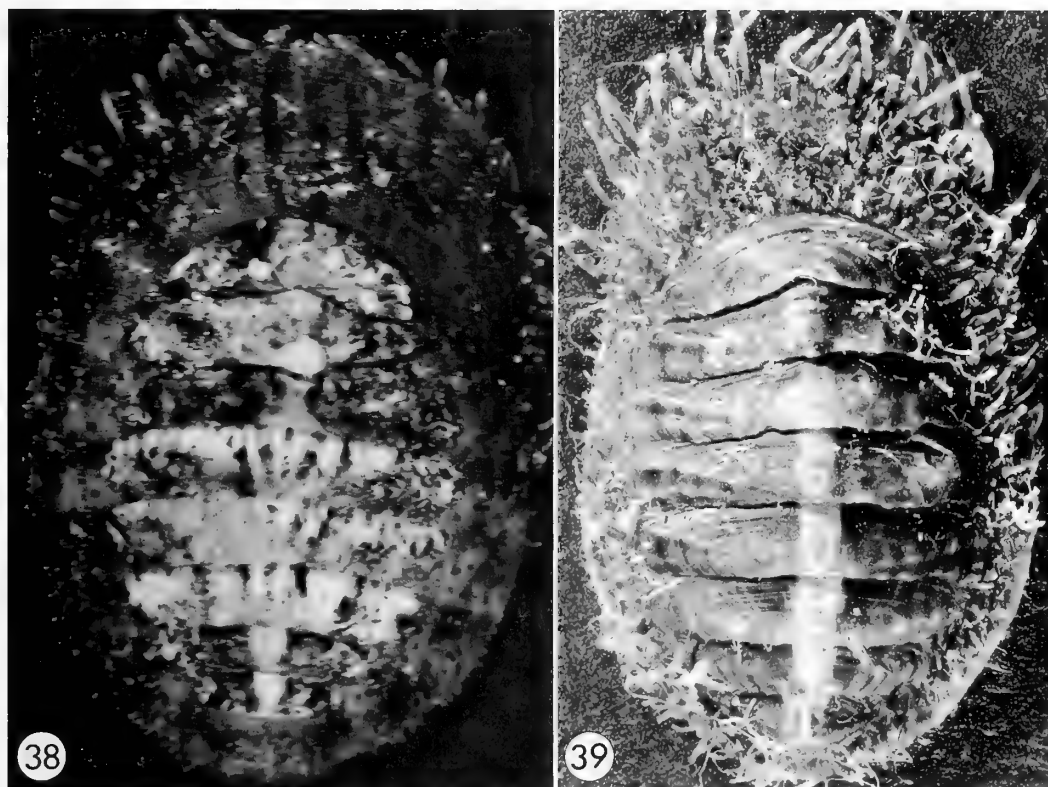
Figures 34, 35. *Placiphorella mirabilis* Clark, sp. nov. Figure 34, Seta; bar = 0.5 mm. Figure 35, Spicule of seta; bar = 100 μ m.

Figures 36, 37. *Placiphorella hanselmani* Clark, sp. nov. Figure 36, Seta; bar = 0.5 mm. Figure 37, Scale of seta; bar = 250 μ m.

ticulamentum about half width of valve v tegmentum; anterior margin sharply convex, without false beak; mucro posterior and slightly raised, with shallow sinus; anterior area smooth except for growth lines, convex anterior of mucro; lateral ribs raised and smooth, posterior area depressed; sutural laminae broad, truncated anteriorly, separated by jugal sinus; insertion teeth very short; with one slit per side.

Girdle: Perinotum covered with scaled bristles (Figure 36) in several series and sizes, largest at about midpoint of girdle, of which there is one adjacent to each suture,

and five around anterior valve, a smaller series in the sutures, and a similar series near the outer margin, other bristles of various sizes randomly scattered; bristle scales (Figure 37) elongated, tapered, truncated distally, with sharp spicule at distal end, about 250 μ m long and 75 μ m wide. Hyponotum densely covered with minute, narrow, smooth, outwardly directed, pointed scales about 10–20 μ m long from suture of valve i and ii to anal region, largest near pallial fold, becoming smaller toward outer margin, like velvet in appearance under moderate magnification; anterior flap with very sparsely placed, minute scales, about



Explanation of Figures 38 and 39

38. *Placiphorella stimpsoni* (Gould, 1859). Whole animal, RNC 387. Katakura, Shimane Peninsula, Honshu, Japan, 0.5–2 m. 38.0 mm × 26.0 mm.

Figure 39. *Placiphorella borealijaponica* Saito & Okutani, 1989. Whole animal, RNC 124. Vostok Bay, Sea of Japan, Russia, 15 m. 23.5 mm × 15.0 mm.

20 μ m long, similar to those on rest of hyponotum, also uniformly covered with tiny papillae, usually coalescing in a vermicular pattern; margin of girdle fringed with narrow, sharp, longitudinally striated spicules about 50 μ m long.

Pallial fold well developed, incised posteriorly, modified anteriorly into numerous precephalic tentacles, about 20 in adults, largest in center, becoming gradually smaller toward edges. Gills holobranchial, extending from valve ii to valve vii.

Radula: (Figure 25) (paratype, CAS 075732) 5 mm long, with about 52 rows of mature teeth; rachidian tooth elongated-heart-shaped, broadened proximally; spatulate uncinals about uniform in width along entire length, outside edge rounded at distal end, inside edge straight.

Type locality: Bahía de Los Ángeles, Baja California Norte (Gulf of California), Mexico (28°57'N, 113°32'W), 0–5 m on bottoms of cobbles.

Type material: Holotype, LACM 2707 (leg. Carl & Laura Shy; intertidal; May, 1976); paratypes: 1, LACM 2708 (same data as holotype); 1, SBMNH 35628 (leg. F. B.

Howerd; intertidal; May 1960); 1, CAS 075732, Puerto Don Juan, S end of Bahía de Los Ángeles, 5 m (leg. Antonio J. Ferreira; SCUBA; 5 October 1984); 2, G.A. Hanselman collection, San Diego, California, Turtle Pin Cove, Isla Smith, Bahía de Los Ángeles, 1 m (leg. G.A. Hanselman; 12 May 1976); 1, G.A. Hanselman collection; Isla Pata, Bahía de Los Ángeles, 0.5–1 m (leg. G.A. Hanselman; 12 May 1976).

Two additional, non-topotypic paratypes: 2, RNC 386 and 512, Puerto de Lobos, Sonora, Mexico, intertidal (leg. Thomas C. Rice; 25 April 1979).

Additional material: MEXICO: G.A. Hanselman collection; Bahía de Los Ángeles, dredged, 21–39 m (leg. Paul and Carol Skoglund; May 1976); 1, CAS 017719, Cholla Bay, Sonora (collector and date unknown). Carol Skoglund (personal communication, September 1992) reports “a few” specimens from Puerto de Lobos and Puerto de la Libertad, Sonora, Mexico (color slide of juvenile, 11.0 mm in length from the latter locality: CAS color slide collection, AJF 491/6).

Distribution: Restricted to the upper Gulf of California,

north of 28°N latitude, where it has been collected at several localities in Bahía de Los Ángeles (the type locality) on the Baja California peninsula side, and Puerto de Lobos and Puerto de la Libertad on the mainland side.

Habitat: *Placiphorella hanselmani* is found on bottoms of medium-sized to large cobbles and boulders lightly bedded in the substrate, from the low intertidal to about 39 m.

Remarks: *Placiphorella hanselmani* is morphologically similar to both *P. velata*, with which it has been confused, and *P. blainvillii*, but may be distinguished from both of these species by: (1) scales of setae, which are about 2.5 times as long as wide, distally truncated, and bear a long, sharply pointed spicule at the distal end; (2) the heart-shaped rachidian tooth of the radula, which is very broad at the working end; (3) the consistent color pattern.

Etymology: Named after George A. Hanselman, of San Diego, California, who has guided and inspired much of my work.

DISCUSSION

Two additional species of *Placiphorella* occur in the shallow waters of northeast Asia, *Placiphorella stimpsoni* (Gould, 1859) and *Placiphorella borealijaponica* Saito & Okutani, 1989. These two species (along with *P. borealis* Pilsbry, 1893) were recently treated by Saito & Okutani (1989).

Placiphorella stimpsoni (Figure 38) is morphologically similar to *P. velata*, *P. blainvillii*, and *P. hanselmani*, but may be easily distinguished from all of them by: (1) setae scales, which in *P. stimpsoni* are very long (up to 350 μm), weakly striated distally, and bear a short spicule at the tip; (2) color of valves whitish, irregularly streaked and mottled with pink, brown, black, and blue-green.

Placiphorella stimpsoni is distributed in Japan from southern Hokkaido (Sea of Japan), along the Pacific coast to Kyushu (East China Sea) in the littoral and shallow sublittoral zones (Saito & Okutani, 1989). It has also been reported in western Korea from Karorim Bay to Hataedo (Yellow Sea) in the shallow subtidal (Dell'Angelo et al., 1990). Reports of *P. stimpsoni* from Russian waters are misidentifications *P. borealijaponica*. Reports of *P. stimpsoni* from North American waters (Dall, 1921; Oldroyd, 1927; Bernard, 1967; Burghardt & Burghardt, 1969; Abbott, 1974; Putman, 1980) are misidentifications of *P. velata* and *P. mirabilis*. *Placiphorella japonica* (Dall, 1925) is a synonym.

Material examined: JAPAN: 2, RNC 387, Katakai, Snimane Peninsula, Honshu, 1, CAS 031637, Sagami Bay, Honshu, 1, CAS 078506, Hiroshima Prefecture, Honshu, 1, CAS 080694, Sagami Bay, Honshu; 1, CAS 082595, Wakayama Prefecture, Honshu. KOREA: 1, CAS 014407, Chinhae; 1, RNC 1500, Karorim Bay.

Fossil valves of *Placiphorella stimpsoni* have been found in the Pleistocene deposits of the Boso Peninsula (near Tokyo), Honshu, Japan (Itoigawa et al., 1976).

Placiphorella borealijaponica (Figure 39) is morphologically similar to *P. borealis*, but may be distinguished by: (1) lack of radial ribs (or sulci) on the head valve; (2) scales of the setae in which the distal half forms three low, distally converging lobes, truncated at the distal end and bearing a short, broad spicule (the setae scales of *P. borealis* bear numerous striations along the distal half and a short, broad spicule at the end); (3) valves sometimes bearing whitish or pale blue-green streaks on the latero-pleural areas; (4) interior of valves tinted blue-green.

Placiphorella borealijaponica is distributed in Japan from northern Hokkaido (Okhotsk Sea), to the north end of Honshu (Saito & Okutani, 1989) and along the Japan Sea coast of Russia, and the southeast (Tartar Strait) coast of Sakhalin Island. Reports of *P. stimpsoni* in Russian waters (Yakovleva, 1952; Sirenko, 1976; Sirenko, 1985) are referable to this species.

Material examined: RUSSIA (JAPAN SEA): 7, LACM 91-91.1, Vostok Bay; 2, RNC 96, Vostok Bay; 2 RNC 124, Vostok Bay; 3, CAS 014408, Vostok Bay; 1, CAS 078434, Sudzuche Bay. JAPAN: 1, RNC 732, Hokkaido; 1, CAS 066637, Oshoro, Hokkaido; 1, CAS 066406, Oshoro, Hokkaido.

Fossil valves of *P. borealijaponica* have been reported from Pleistocene deposits of the Boso Peninsula, Honshu (as *P. japonica*) (Itoigawa et al., 1976).

Key to the genus *Placiphorella*

Dall, 1879, ex Carpenter MS

- 1a Valves dark brown (may be streaked with light brown, white or pale blue-green) with whitish jugal stripe 2
- 1b Color of valves not as above 3
- 2a Head valve with numerous low, radiating ribs; valves unstreaked; interior of valves white
..... *P. borealis* Pilsbry, 1892
- 2b Head valve without low radiating ribs; valves often streaked; interior of valves light blue-green (Japan, Russia)
..... *P. borealijaponica* Saito & Okutani, 1989
- 3a Valves uniform in color 4
- 3b Valves not uniform in color 5
- 4a Valves reddish (head valve may be paler)
..... *P. rufa* Berry, 1917
- 4b Valves white (Cosmopolitan)
..... *P. atlantica* (Verrill & Smith, 1882)
- 5a Setae restricted to periphery of girdle and around head valve (the latter often absent); scales of setae tapering to a point distally and bearing latticelike sculpturing (California, Baja California)
..... *P. mirabilis* Clark, sp. nov.
- 5b Setae and scales of setae not as above 6
- 6a Scales of setae 200–260 μm in length, smooth, cylindrical, and distally pointed (Central and South America) *P. blainvillii* (Broderip, 1832)

- 6b Scales of setae not as above 7
 7a Scales of setae very large (up to 350 μm in length);
 distal end weakly striated and bearing a short
 spicule (Japan, Korea)
 *P. stimpsoni* (Gould, 1859)
 7b Scales of setae smaller and not distally striated .. 8
 8a Scales of setae 190–200 μm in length, 40–45 μm
 in width; distal end rounded and bearing a short
 spicule *P. velata* Dall, 1879, ex Carpenter MS
 8b Scales of setae 250 μm in length, 75 μm in width;
 truncated distally and bearing a large spicule
 (Gulf of California)
 *P. hanselmani* Clark, sp. nov.

ACKNOWLEDGMENTS

For making their collections and records available for this study, I thank James H. McLean and the late C. Clifton Coney (LACM); Elizabeth Kools and Robert Van Syoc (CAS); Dory Vardes (ANSP); Paul H. Scott (SBMNH); Philip Lambert and Gordon Green (RBCM); Piet Kaas (RMNH); Bruce L. Wing (NMFAB); the late Richard S. Houbbrick and Shelly Greenhouse (USNM); Boris I. Sirenko (ZIAS); Geerat Vermeij (UCD); Nora R. Foster (UAF); Ian McTaggart Cowan, Victoria, British Columbia; George A. Hanselman and Jules and Carol Hertz, San Diego, California; Bruno Dell'Angelo; Prato and Donald R. Shasky, Redlands, California. For help with the literature, I thank Douglas J. Eernisse, University of Michigan, Ann Arbor; Lindsey T. Groves (LACM); Thomas C. Rice, Port Gamble, Washington; George P. Holm, Richmond, British Columbia; and Atsushi Naruse, Mizunami City. For help with the scanning electron microscopy, I thank Darlene Southworth, Southern Oregon State College, Ashland, Oregon. For drawings, I thank Piet Kaas (RMNH). For help with arranging loans of museum material, I thank Marvin J. Coffey and Darlene Southworth (SOSC). For help with field work, I thank Alan J. Murray, David Zwick, and Kurt Morin, Ketchikan, Alaska. For helpful commentary, I thank James H. McLean (LACM); George A. Hanselman, San Diego, California; and two anonymous reviewers.

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A New Species of *Okenia* (Nudibranchia: Doridacea) from the Peruvian Faunal Province

by

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Abstract. A new species of *Okenia*, with a smooth dorsum, white body, and yellow markings, has been found in Peru and Chile in the shallow subtidal. This species is described and compared to similar species worldwide. This is the first record of the genus from the Peruvian faunal province.

INTRODUCTION

The eastern South Pacific opisthobranch fauna of the Peruvian province is poorly known. The first report was that of Lesson (1831) who briefly described and figured *Aeolidia lottini* from Talchuano, Chile, near the southern end of the Peruvian faunal province. Of greater impact were the descriptions and excellent drawings of d'Orbigny (1835-1846) of 14 new species of opisthobranchs from the coast of Peru and Chile. These works were followed by Couthouy's manuscript descriptions of three species from central Chile, published by Gould (1852), which are inadequate for proper identification. Bergh (1873) described an aeolid,

Aeolidia serotina, collected by Professor Kroyer and deposited in the Copenhagen Museum. Bergh (1898) described 10 additional species which had been collected by L. Plate in Chile. Dall (1908) described *Scaphander cyllindrellus* from Callao, Peru. Odhner (1921) added *Aeolidia collaris* and *Cadlina sparsa* from Juan Fernández Island. The latter species has subsequently been reported as far north as San Francisco, California. The last opisthobranch researcher to visit the Peruvian faunal province was Ernst Marcus (1959), who described a sacoglossan, *Aplysiopsis brattstromi*, from northern Chile and another nine new species from the Gulf of Ancud, an area of faunal overlap just south of the 41°S boundary of the Peruvian and Magellanic faunal provinces. This description of a new species of *Okenia* Menke, 1830 is the first description of a new species of opisthobranch from the Peruvian faunal province since 1959 and the first report of the genus *Okenia* from the eastern coast of the South Pacific.

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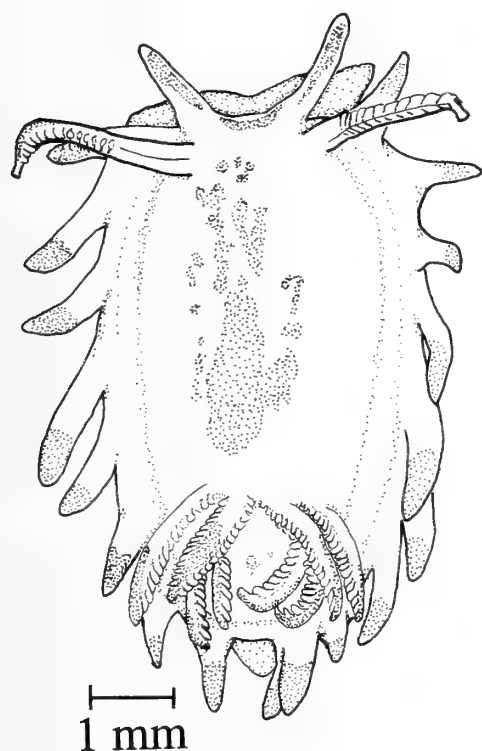


Figure 1

Okenia luna Millen, Schrödl, Vargas & Indacochea, sp. nov.
 Drawn from a photograph of a living specimen.

SYSTEMATICS

Family GONIODORIDIDAE
 H. & A. Adams, 1854

Genus *Okenia* Menke, 1830

Okenia luna Millen, Schrödl,
 Vargas & Indacochea, sp. nov.

(Figures 1–9)

Etymology: The rounded shape and pale white and yellow coloration suggested the Latin (and Spanish) word for moon.

Material: Holotype: California Academy of Sciences CAS-IZ 089293, 1 specimen, 7 mm long. Collected by Michael Schrödl on 17 April 1992; Bay of Coliumo, just north of Concepción, central Chile (36°32'S, 73°57'W), at 12 m depth on the alga *Gracilaria chilensis* Bird, MacLachlan & De Oliveira, 1987, covered with hydroids and the bryozoan *Alcyonidium nodosum* O'Donoghue & de Waterville, 1944.

Paratypes: CASIZ 089294, 4 specimens, 5–7 mm long. Collected by M. Schrödl on 2 May 1992 at the type locality, 12 m depth on the alga *Gracilaria* and on *Nassarius* shells on a muddy sand bottom.

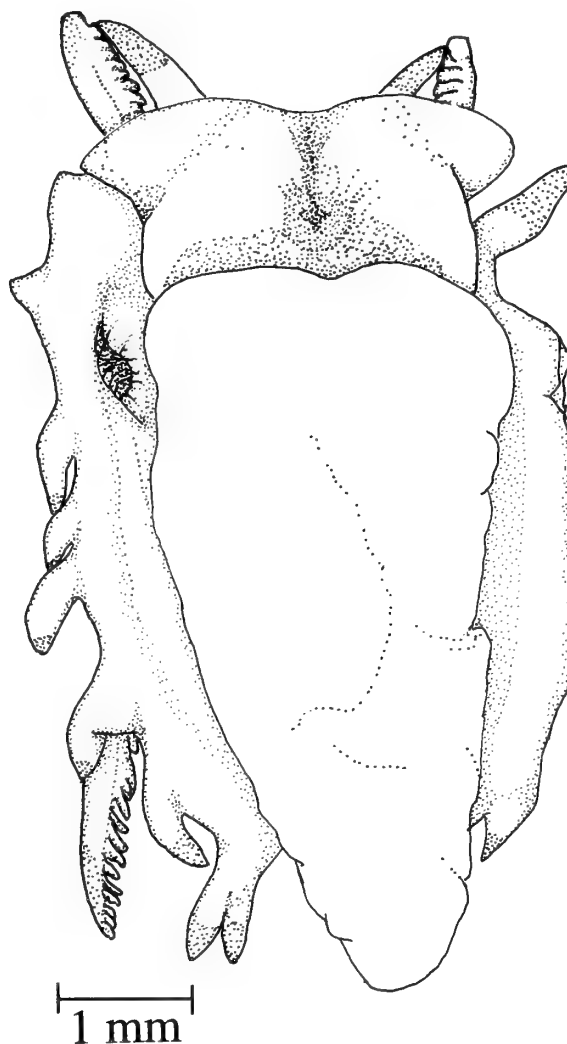


Figure 2

Okenia luna Millen, Schrödl, Vargas & Indacochea, sp. nov.
 Camera lucida drawing of the ventral view of a preserved specimen.

University of San Marcos, Lima, Peru, 1 specimen, 3.5 mm long, in the collection of Dr. Carlos Paredes. Collected on 5 May 1987 on algae at Ancón, Peru (11°47'S, 77°11'W).

Museo de Historia Natural de la Universidad Ricardo Palma, Lima, Peru, RPT 112–117, 6 specimens, 4.5–10 mm long. Collected by Aldo Indacochea on 30 November 1993; Ancón, Peru, 3 m depth on the algae *Gracilaria* and *Ulva* encrusted with bryozoans.

Museo Zoológico de la Universidad de Concepción, Concepción, Chile MZUC 22522, 1 specimen, 7 mm long. Collected by M. Schrödl on 2 May 1992 at the type locality, 12 m depth on the alga *Gracilaria*.

Additional material: One specimen collected in Ancón, Peru on 30 June 1988 was dissected. One hundred and

twenty-one living specimens were observed from March to May, 1992 in the Bay of Coliumo, Chile, and five were dissected.

Description: *External morphology:* The living animals are 5–12 mm long, 3–5 mm wide, and 2.5–5 mm high, with a mean length of 8.4 mm ($n = 127$). They are elongate oval in shape (Figure 1), with an overhanging mantle rim 1 mm wide. The mantle rim has 7–12 simple, 1–1.5 mm long, digitiform processes per side. In living animals, these usually curl upward. Anteriorly the overhanging rim is discontinuous. The first process on each side is anterior to the rhinophores, and projects anteriorly. The two most posterior processes on each side are longer than those on the sides and join at their bases, sometimes fusing along most of their length with only the tips separate.

The dorsum is smooth, with neither crests nor tubercles. When contracted, it appears slightly pustulose. The mantle processes do not contain obvious spicules. The rhinophores, which are curved back over the dorsum in living animals, are up to 3 mm long. They bear 10–15 perfoliate lamellae which meet in a chevron on the posterior surface. Anteriorly they are smooth, and they end in a blunt tip.

The 7–11 (usually nine) simply pinnate gills are arranged in a wide semicircle around a small central anal opening. The renal pore is to the right of the anus. The gills are larger anteriorly, up to 2.5 mm long; the posteriormost are sometimes very small. They are irregularly laminate with 16–20 lamellae per side, positioned toward the interior edge. The basal third of the central rachis contains internal branchial glands.

The head (Figure 2) is in the form of a bilobed velum. The tentacles are broad, flattened triangles extending laterally and not demarcated from the head. The foot is straight or slightly indented in the midline, but unnotched anteriorly. The anterolateral corners are rounded, and the entire foot tapers to a rounded, leaflike tail. The foot flange is 0.5 mm wide and is hidden by the mantle rim. The tail projects up to 1.5 mm beyond the body wall.

The ground color of the body is hyaline white. The mantle processes are yellow on the outer half, ending in clear tips. There is a broad mid-dorsal stripe made up of yellow spots, starting behind the rhinophores and ending before the gills. There is a lateral yellow line between the anteriormost mantle processes, sometimes connecting as a

yellow streak across the entire front of the mantle margin, occasionally reduced to a wide lateral dash or triangle in the center. In a few specimens, the yellow spots on the mantle are replaced wholly or partially by opaque white. The rhinophores have hyaline white bases and pale cream leaves. Opaque white pigment extends from the tips down the central rachis about one-fourth of its length and occasionally is extended to the mid-rhinophore region by yellow pigment. It is more obvious on the anterior where it is not obscured by the leaves of the rhinophores. The gills are hyaline white with a yellow streak one-half to two-thirds of the way down from the tip on the outer side. The sides, foot, and head are hyaline white, usually without pigment, although a few of the 127 specimens examined have an interrupted medial opaque white line on the tail.

Digestive system: The short buccal tube is surrounded on the lateral and ventral surface by simple labial glands. The round lip disc (Figure 3) has two ventral flaps and two ventral semicircular areas composed of rectangular scales, 6.2–9.6 μm long, which have four to six serrations on the outer edges (Figure 4). The buccal bulb has a large, cuticle-lined, sucking crop consisting of two muscular pouches with a median muscular strap between them. A short radular sac projects posteriorly from the ventral surface of the buccal bulb.

The radular formula is 23–27 (1.1.0.1.1). The lateral teeth have a rounded base and a long, almost straight, denticulate hook set nearly at right angles to the base (Figures 5, 6). The hook bears 12–36 denticles on the inner surface (Figure 7). At the inner base of the hook is a small knoblike projection (Figure 5). The lateral teeth have bases 0.06–0.11 mm long and hooks 0.08–0.12 mm long. The marginal teeth are small oval plates with one small hook (Figure 8). They reach a height of 0.03–0.09 mm.

The esophagus is long, tubular, and thin-walled. On either side of the esophagus is a small, flattened, oval, granular salivary gland which attaches to the buccal bulb by a thin duct. The esophagus enters the base of the vertical, oval stomach, which is anterior to the digestive glands and lacks a caecum. The digestive glands are confluent, oval except for the anterior right depression of the reproductive system, and pinkish in preserved specimens. Dorsally they are covered by the cream-colored ovotestis. The intestine exits at the upper right of the stomach in a wide

Explanation of Figures 3 to 8

Figure 3. Lip disc. SEM micrograph showing the ventral flaps and the scale pattern in the ventral left quadrant. Scale bar = 40 μm .

Figure 4. Close-up of lip scales showing the serrated edge. Scale bar = 5 μm .

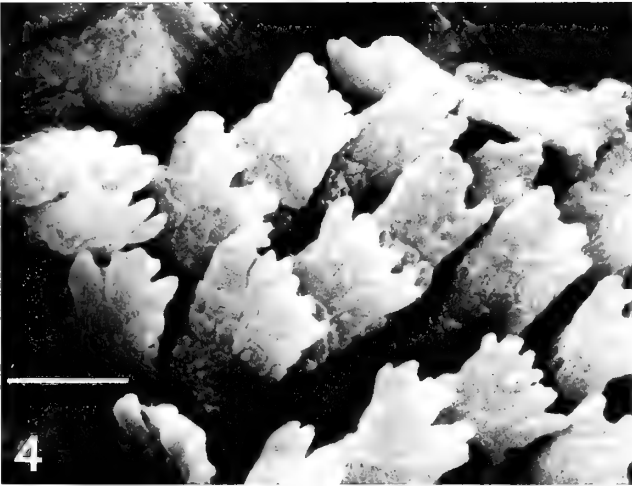
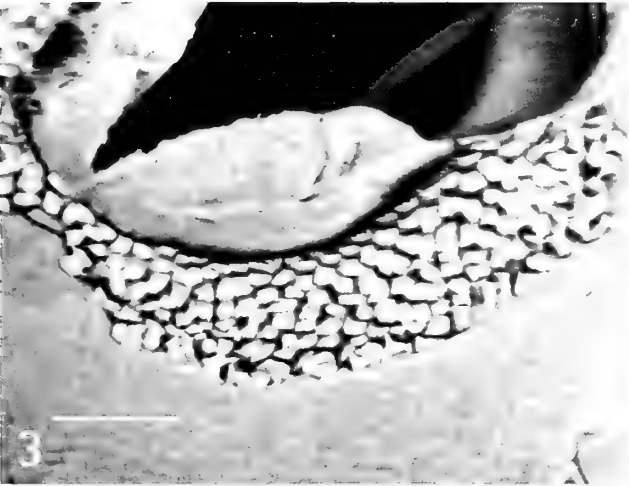
Figure 5. Lateral radular teeth from a half row. Scale bar = 20 μm .

Figure 6. Lateral and marginal teeth. Scale bar = 20 μm .

Figure 7. Close-up of denticles on the lateral teeth. Scale bar = 2 μm .

Figure 8. Marginal teeth. Scale bar = 10 μm .

→



curve and travels on the right side of the digestive gland. Posteriorly it loops to the left to end at the anus in the center of the branchial semicircle. The anal tubercle is low.

Central nervous system: The cerebropleural ganglia are completely fused and joined by a short connective duct. The small rhinophoral ganglia are connected anteriorly by a short stalk. The eyes are on short stalks. A right visceral ganglion is present. The round pedal ganglia are smaller than the cerebropleurals and are located slightly posterior and ventro-lateral to them. They are connected to the cerebropleurals by a very short commissure and to each other by a slightly longer pedal commissure. The paired, oval buccal ganglia lie close together under the esophagus and each has a gastro-esophageal ganglia attached by a short anterior stalk.

Reproductive system (Figure 9): The ovotestes cover the surface of the digestive gland, and the round female lobules are peripheral to the male ducts. There are two major longitudinal collecting ducts which unite to form the long thin preampullar duct, beginning just to the right of the esophagus. This duct widens into a curved, tubular ampulla which runs across the dorsal surface and down the anterior face of the female gland mass. The ampulla divides into a short oviduct which enters the fertilization chamber and the vas deferens. The vas deferens travels dorsally a short distance, then loops anteriorly, widening into a long, tubular prostatic portion which proceeds inwardly and then loops back on itself. It constricts into a thin, tubular muscular portion which is about one-half the length of the prostate. The distal half of the muscular vas deferens is inside a thin penial sheath, which enters a short eversible, conical praeputium. The tip of the vas deferens is armed for 0.135 mm with approximately eight rows of small spines with round bases, 4.5–6 μm long.

The vagina is slightly expanded near its opening posterior to the penis. It is a straight, thin cylindrical tube. It ends in a three-way junction with the ducts from the bursa copulatrix, receptaculum seminis, and the insemination duct, which are vaginally arranged. The duct to the bursa copulatrix is short, wide, and in line with the vagina. The bursa copulatrix is large and circular, the inner sac is dark brown. The duct to the receptaculum seminis runs distally alongside the vagina then curves back on itself to form a small, elongate receptaculum seminis. The insemination duct also runs parallel to the vagina a short distance before crossing the female gland mass and entering the fertilization chamber at the anterior end of the albumen gland. The fertilization chamber is round and swollen with sperm, with an elongate caecum projecting into the mucous gland. The oviduct enters the albumen gland from the round portion next to the entrance of the insemination duct. The female gland mass has a large, granular, oval anterior albumen gland, a highly convoluted mucous gland, which is ventral to the albumen gland, and a small, oval membrane gland ventral and distal to the albumen gland. The exit duct is wide and ventral to the

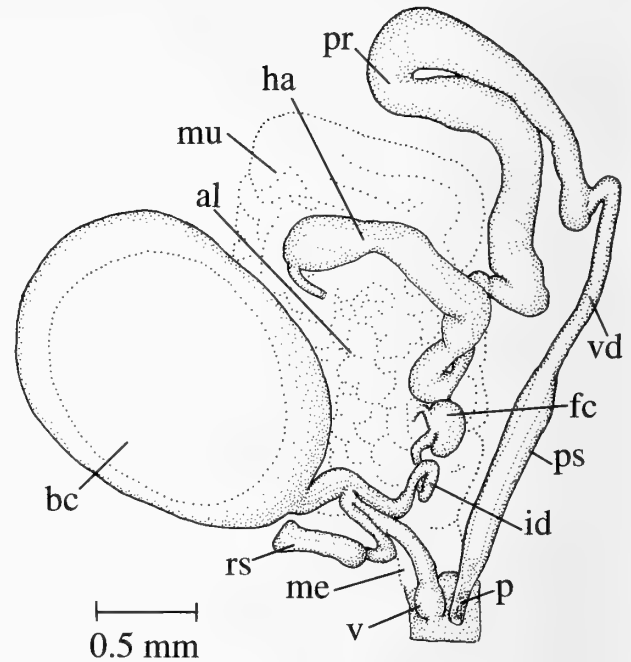


Figure 9

Okenia luna Millen, Schrödl, Vargas & Indacochea, sp. nov. Reproductive system drawn using a camera lucida. Key: al—albumen gland; bc—bursa copulatrix; fc—fertilization chamber; ha—hermaphroditic ampulla; id—insemination duct; me—membrane gland; mu—mucus gland; p—penis; pr—prostate; ps—penis sheath; rs—receptaculum seminis; v—vagina; vd—vas deferens.

vagina. The genital openings are located close to the notum on the right side just posterior to the front of the foot, in the anterior one-third of the body.

Ecology: *Okenia luna* occurs at 3–20 m depth on a variety of substrates; rock walls, mud, and sand bottoms where they are usually on *Argopecten purpuratus* (Lamarck, 1819) shells, *Nassarius* shells, polychaete tubes (*Diopatra* sp.) and algae. These hard substrates were encrusted with the bryozoan *Alcyonidium nodosum*. The nudibranchs were observed feeding on this bryozoan in the laboratory.

Okenia luna has been found in the months of May, June, September, November, and December in central Peru, and from March to May in central Chile, with a sudden disappearance of this species in late May. In mature specimens from Chile, 70 percent have parasitic copepods. Spawn masses were found in December in Ancón, Peru, and in May in central Chile. Spawning appears to be a gregarious behavior; up to 51 specimens laid over 100 spawn masses on three small algal plants within a 15 m-square area. The spawn masses are cream-colored, sausage-shaped strings with $\frac{3}{4}$ to $2\frac{1}{2}$ whorls, approximately 5 mm in diameter. There is one egg per capsule, with a preserved diameter of 90–100 μm . Eggs hatch in 8–11 days at 15–16°C into free-swimming veligers.

The known range of *Okenia luna* is from Ancón, Peru (11°47'S, 77°11'W) to the Bay of Coliumo, near Concepción, central Chile (36°32'S, 73°57'W).

DISCUSSION

This new species of *Okenia* belongs to the group which Bergh (1881) called *Idaliella*. *Idaliella* was characterized by a smooth dorsum, lacking medial notal appendages, and an oral armature consisting of two bands of scalelike armature as opposed to a ring of hooks. Ernst Marcus (1957) pointed out that there are exceptions to the labial armature, with *Okenia impexa* Marcus, 1957 having a smooth ring, and *O. echinata* Baba, 1949 having two bands of armature instead of a complete ring. On this basis, he suggested that the genus *Idaliella* be considered a subgenus. We agree with Robert Burn (1971) that *Idaliella* is not sufficiently distinct and should be regarded as a subjective junior synonym of *Okenia*.

Only three or four of the currently recognized 24 or 25 species of *Okenia* have a smooth notum and two bands of labial armature. Three of these, unfortunately, have their synonymy in dispute. *Okenia quadricornis* (Montagu, 1815), the oldest nominal species, is poorly described and could be a senior synonym to either *O. aspersa* (Alder & Hancock, 1845), or *O. pulchella* (Alder & Hancock, 1854), or both (see Schmekel & Portmann, 1982; Just & Edmunds, 1985; Thompson, 1988). Further confusion has arisen because *Okenia aspersa* apparently can have either a smooth notum or one small mid-dorsal appendage (Just & Edmunds, 1985; Cervera et al., 1991). All of these species can be separated from *Okenia luna* on the basis of their reddish-brown coloration, high subquadrate bodies, and large frontal velum. Three other species, *Okenia amoenula* (Bergh, 1907), *O. mediterranea* (Von Ihering, 1886), and *O. sapelona* Marcus & Marcus, 1967 are similar in shape to *O. luna*, and also have pale bodies with yellow on the notal processes, dorsum, and gills.

Okenia luna can be separated from *O. amoenula* externally by the red pigment which is prominent on the dorsum, gills, tail, mantle processes, and sides of *O. amoenula* (see Gosliner, 1987:fig. 158) and by the wider branchial circlet of *O. luna*. Internally, the scales on the lip disc are larger, smooth, and more elongate in *O. amoenula* (to 0.25 mm vs. 0.001 mm), and there are more radular tooth rows (32–35 vs. 23–27) (Bergh, 1907). According to MacNae (1958), the reproductive bursae are semi-serially arranged in *O. amoenula*. They are vaginal in *O. luna*, and the receptaculum seminis is much smaller and more elongate, with a longer stalk.

Okenia mediterranea differs from *O. luna* in its possession of a low median keel-shaped crest with four to five small tubercles and in having two to four small lateral tubercles in a line on each side of the central crest (Cervera et al., 1991). *Okenia mediterranea* is usually colored with both yellow and light-red pigment, giving it an orange color,

but a few individuals have only yellow (Cattaneo-Vietti et al., 1990: pl. 1, fig. 3). The yellow pattern described by Schmekel (1979) varies from that of *O. luna*, which lacks yellow on the sides of the notum and tail. The reproductive system described by Cervera et al. (1991) differs from that of *Okenia luna* in that the ampulla is much shorter, the bursae are serially arranged, and the seminal receptacle is larger and oval in shape, with a short duct. In addition, the prostate is shorter and wider, and the albumen gland smaller in *Okenia mediterranea*.

Okenia sapelona is similar to *O. mediterranea* in its possession of a low central crest of five small tubercles and two pairs of lateral tubercles on each side (Marcus & Marcus, 1967). This distinguishes it from the smooth medial notum of *Okenia luna*. *Okenia sapelona* differs also in color, the ground being iridescent pale blue, and the gills and rhinophores having maroon spots. The yellow pattern is spread over the sides of the notum, tail, sides, and top of the head, places where it is absent in *Okenia luna*. The gill circlet is much smaller in *Okenia sapelona* than in *O. luna*. Internally, *Okenia sapelona* has a complete labial circlet with smooth octagonal plates which are conical in side view (Marcus & Marcus, 1967), not the rectangular plates with serrated edges found in *O. luna*. It has fewer radular teeth (12 vs. 23–27). The reproductive system has serially arranged bursae, and the receptaculum seminis is larger and more oval than that found in *Okenia luna*. It is possible, from the external similarities and the reproductive features, that *Okenia sapelona* from Georgia, in the western North Atlantic, and *O. mediterranea* from the Mediterranean Sea may prove to be conspecific and amphiatlantic in their distribution.

ACKNOWLEDGMENTS

We would like to thank Dr. Carlos Paredes, University of San Marcos, Lima, Peru for access to his opisthobranch collection. We also thank Dr. Moyano, Concepción University, for his bryozoan identification and S. Gigglinger for his assistance in SCUBA diving. We would like to acknowledge the Marine Biological Station, Concepción University, Concepción, Chile for the use of its facilities. This research was funded by the Department of Zoology, University of British Columbia.

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NOTES, INFORMATION & NEWS

Shell Strength of the Non-indigenous Zebra Mussel *Dreissena polymorpha* (Pallas) in Comparison to Two Other Freshwater Bivalve Species

by

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Introduction

In 1988, the non-indigenous zebra mussel, *Dreissena polymorpha* (Pallas), was first collected in Lake St. Clair, Michigan (Hebert et al., 1989). This freshwater bivalve, presumably brought into this country in ballast water of an oceangoing vessel, is common throughout much of Europe and probably originated in the Black, Caspian, and Azov seas (Mackie et al., 1989). Fertilization is external; after being carried passively in water for several weeks, larvae settle and attach tenaciously with proteinaceous byssal threads to virtually any surface (Mackie et al., 1989). This trait, coupled with its ability to tolerate extreme crowding, has made this species a serious biofouler in North America.

Heavy infestations of zebra mussels have clogged pipes and valves, and have fouled cable and machinery at power facilities, pumping plants, and navigation vessels along the Great Lakes (Nalepa & Schloesser, 1993). Added mass of zebra mussels can cause structural damage to concrete walls and gates on locks, dams, and drainage structures. By early 1993, this species had been found in the Illinois, Ohio, Mississippi (from Wisconsin to New Orleans), Cumberland, Tennessee, and Kanawha rivers (Miller, unpublished information).

Kennedy & Blundon (1983) analyzed shell strength of the Asian clam, *Corbicula fluminea* (Müller), a non-epiphytic macrofouler that lives within the upper few centimeters of sand and gravel substratum. The purpose of our paper is to present information on shell morphometrics and forces required to crack zebra mussel shells. Forces required to crack shells of zebra mussels are compared with *C. fluminea*, as well as a native freshwater mussel with an extremely thick shell, the ebony shell *Fusconaia ebena* (I. Lea). Information on shell morphometrics and forces required to crack shells can be used to determine the vulnerability of *D. polymorpha* to predation by crayfish, fish, or waterfowl, as well as the susceptibility of equipment along waterways to infestation.

Materials and Methods

Zebra mussels were collected from the concrete wall of Black Rock Lock in Buffalo, New York, in March 1992 and shipped by air to the laboratory for immediate processing. *Corbicula fluminea* and *F. ebena* were collected by divers at a gravel shoal at Ohio River Mile 967 near Cairo, Illinois, in August 1992 and returned to the laboratory for immediate analysis.

The compressional force required to crack shells was determined and recorded with an Instron 4206, a microprocessor-controlled closed-loop materials testing system. Mussels with shells that were suspected to require less than 4000 Newtons were evaluated with a 5000 Newton, internally calibrated, load cell. Stronger shells were tested with a 150,000 Newton capacity cell. Specimens were evaluated with either of two interchangeable upper compression platens, either 50 or 150 mm depending upon shell dimensions. Force was applied continuously and without shock at a rate of about 240 mm per minute. When the instrument detected shell cracking, force was removed. The peak force required to crack the shell was recorded using a data acquisition system.

Before testing, each mussel was placed on its side (lengthwise) with dorsal aspect pointing away from the operator. No special cleaning or preparation was required. The total number tested, minimum, and maximum shell length for individuals of the three species tested were: *D. polymorpha* (35, 4.1–20.3 mm); *C. fluminea* (50, 9.5–38.2 mm); and *F. ebena* (53, 10.3–75.0 mm). Shell length was measured with a digital caliper, and shell thickness of the right valve immediately adjacent to the umbo was measured with a Mitutoyo Digimatic Micrometer.

A sample of 50 zebra mussels was used for morphometric analyses. Total shell length was measured, and mass in air was determined with an electronic balance. Mass in water was measured with a wire basket suspended from the balance pan and submersed in a beaker of water. Water volume displaced was estimated using a 10 mL graduated settling tube. Regression equations for each relationship were developed after separating similarly sized mussels into approximately 10 groups.

Results and Discussion

Dreissena polymorpha had a significantly weaker shell than either *C. fluminea* or *F. ebena* (Figure 1). About 22 Newtons were required to crack a 20-mm-long zebra mussel shell. Forces of 118 and 806 Newtons were required to

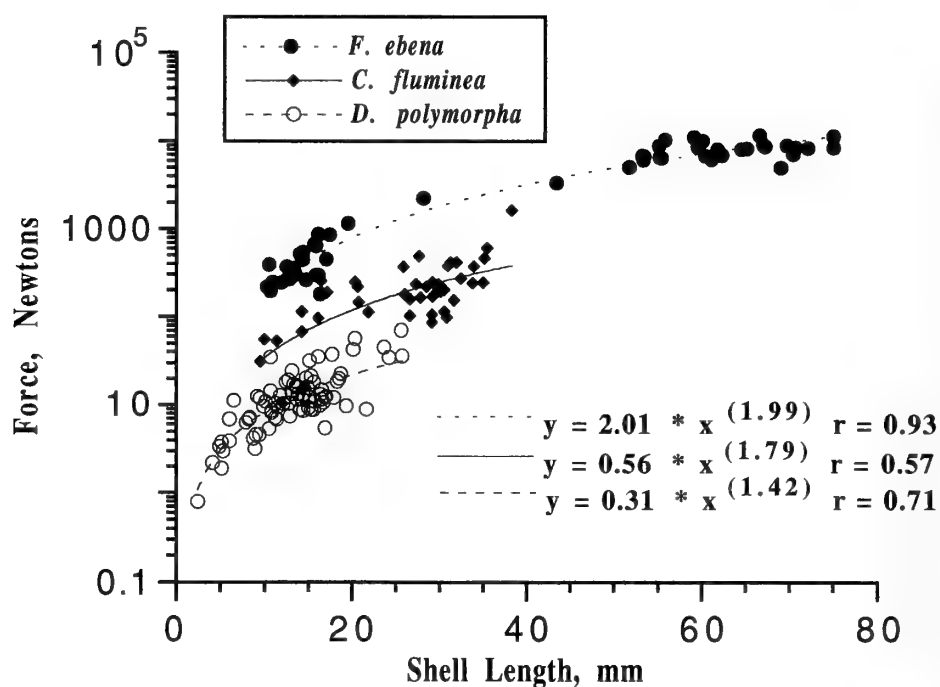


Figure 1

Force in Newtons required to crack shells of *Dreissena polymorpha*, *Corbicula fluminea*, and *Fusconaia ebena*.

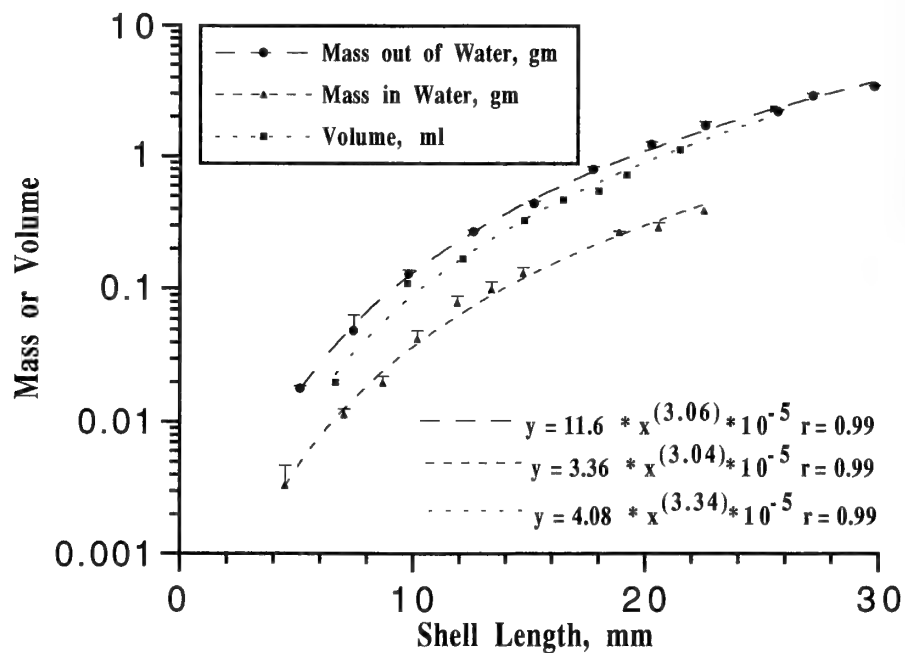


Figure 2

The relationship between shell length (mm) and total mass in and out of water (g) and total volume (cm³) of the zebra mussel, *Dreissena polymorpha*.

crack 20-mm-long shells of *C. fluminea* and *F. ebena*. A 75-mm-long shell of *F. ebena* was cracked with a force of 11,260 Newtons.

Slopes for all species were significantly different ($P < 0.05$, Sokal & Rohlf, 1981). The slope of the regression line for *F. ebena* was significantly different from *C. fluminea* ($F = 51.2$) and *D. polymorpha* ($F = 64.7$). The slope of the regression line relating *C. fluminea* to *D. polymorpha* was also significant ($F = 15.2$). Shell strength was directly related to shell thickness. A 20-mm-long shell of *D. polymorpha* was 0.31 mm thick. A similarly sized *C. fluminea* and *F. ebena* shell was 1.3 and 3.0 mm thick, respectively.

In a similar study of *C. fluminea*, Kennedy & Blundon (1983) regressed \log_{10} force (Y) on \log_{10} length (X) and fitted the regression line: $\log Y = 1.96 \log X - 0.30$. Converting logarithms of their equation to powers yielded $Y = 0.501X^{1.96}$. The slope of our regression line (1.79) is slightly less than that of Kennedy & Blundon (1983), although intercepts are similar (0.501 for the previous workers and 0.56 for this study). Using the equation of Kennedy & Blundon (1983), a 20-mm-long *C. fluminea* shell would be cracked with a force of approximately 177 Newtons. The previous workers obtained their specimens from the Potomac River, Whites Ferry, Maryland. Differences in shell strength were unrelated to calcium content of the water. Mean dissolved calcium (mg/liter) was 33.2 ($n = 17$) and 33.4 ($n = 16$) at a gaging station on the Potomac (at Washington, D.C.) and Ohio (near Grand Chain, Illinois) rivers between October 1989 and the summer of 1992 (U.S. Geological Survey Water Supply Water Quality Records, Towson, Maryland and Louisville, Kentucky).

In Europe, zebra mussels are eaten by diving ducks (Draulans, 1987), crayfish (Piesik, 1974), and fish (Budzynsha et al., 1956; Daoulas & Economidis, 1984). Kennedy & Blundon (1983) concluded that Asian clams greater than 6 mm total shell length could not be cracked by the crayfish *Procambarus clarkii* (Girard) which exerts a force of 9.9 Newtons at the base of its chelipeds (Brown et al., 1979). Our results indicate that a force of 9.1 Newtons is sufficient to crack a *D. polymorpha* shell 13 mm long. Because of their comparatively weaker shell, zebra mussels about twice the length of *C. fluminea* will be susceptible to predation by *P. clarkii*.

Compared to other bivalves, *D. polymorpha* has a relatively fragile shell that can be easily cracked and broken by operation of gates, valves, winches, or cleaning equipment. Although this species can quickly infest and render equipment inoperable, maintenance personnel will find it extremely susceptible to damage from normal operations and mechanical cleaning procedures.

A 20-mm-long zebra mussel has a mass of 1.20 g and displaces a volume of 0.87 cm³; its mass in water (0.34 g) is about 33% its mass in air (Figure 2). Factors to calculate the total mass of zebra mussels in and out of water were

0.34 and 1.20 times total volume, respectively. Factors were developed for populations consisting of equal numbers of juveniles (individuals less than 10 mm total shell length) and adults. A 1 m square surface coated with a 2 cm thick layer of zebra mussels (20,000 cm³) weighs 6.8 kg in water and 24 kg out of water. Conversion factors can be used to estimate stress to equipment or materials infested with zebra mussels; winches and certain other structural components are usually overdesigned within narrow limits.

Acknowledgments

Research was funded by the Zebra Mussel Research Program of the U.S. Army Corps of Engineers. Sarah Wilkerson and Geralline Wilkerson prepared specimens and Mr. Fred Causy operated the Instron testing machine. Authors thank Mr. Jim Boyle and Mr. Gary Dye for collecting and sending zebra mussels and two anonymous reviewers for constructive comments. Permission was granted by the Chief of Engineers to publish this information.

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BOOKS, PERIODICALS & PAMPHLETS

Camaenid Land Snails from Western and Central Australia

(Mollusca: Pulmonata: Camaenidae).

VI. Taxa from the Red Centre

by ALAN SOLEM. 1993. Records of the Western Australian Museum, Supplement No. 43. pp. 983-1459.

This, the sixth part of a series that began in 1979 with Rec. West. Austral. Mus. Supplement No. 10 ("... I. Taxa with trans-Australian distribution"), adds another major block to the late Alan Solem's edifice of descriptive land malacology. Part VII is still being prepared. Camaenid land snails form a notable exception to the generalization that the arid Red Centre of Australia has not been a region of evolutionary radiation. The Sinumeloninae are represented by eight genera and 35 species (19 of the species newly described herein); the Pleurodontinae are represented by four genera and 30 species (20 new herein).

The illustrations—SEM photographs of jaws, radula, and shell sculpture; drawings of shells and reproductive system anatomy—are of the usual high quality that one associates with Solem's work. The descriptive text is typical of that which set the standard for land snail description for many years.

One statement candidly declares Solem's systematic method—or at least what he did *not* do: "The systematic analysis involved neither cladistics or phenetics. As often pointed out in this study, the Red Centre camaenid fauna consists of two very different subfamily groups. Conchological convergence between the sinumelonine genus *Mon-tanomelon*, gen. nov., and the pleurodontine genus *Semotrachia* was so extensive that the former's affinities were not recognized until the final dissection work. There are no clear polarities of structure or the unidirectional character changes developed that would permit such simplistic electronic modeling of phylogeny. Most changes in structure seem to have multiple origins" (p. 991). Given his time and place in malacology and his extensive experience in hands-on description of land snails, it is easy to see why Solem would trust his own sense of how things were, over the seemingly faceless protocols of phylogenetic analysis. (Interestingly, at least one grant proposal late in his career included provisions for cladistic analysis.) Yet, for another category of pulmonate systematists, none of these excuses holds up: if the fauna consists of two "very different" groups that together do not constitute a clade (apparently they do not, as the Neotropical Pleurodontinae seem to be the sister group of the Australian Pleurodontinae), then two separate analyses can be performed. In the absence of "clear polarities," character states can be submitted as unpolarized, or the argument can be based on outgroup

comparison. "Most changes in structure seem to have multiple origins" implies that Solem had in mind some sense of polarities; better estimates of the extent and pattern of homoplasy could be obtained by phylogenetic analysis. Solem's declaration sells short the ability of PAUP, MacClade, and other software to report homoplasy as such; in fact, they are extraordinarily good at it. More significantly, it ignores the importance to systematics of generating testable hypotheses of relationship.

Actually, very little of this monograph is devoted to "systematic analysis" in the sense of breaking down the kinship relations among species, genera, and suprageneric groups. Pp. 997-998 assert the monophyly of Old World and New World Camaenidae. The subfamily Pleurodontinae is said to occur in both regions and a number of similarities enumerated between Neotropical and Australian genera. These include closely observed details, such as the angle at which the free oviduct enters the spermathecal-vaginal tract. Other characters, differing between New and Old World Pleurodontinae, are dismissed as trivial, sometimes with seemingly ad-hoc adaptive explanations ("Dominica has a far wetter climate than the Red Centre"). The so-called "head-wart," a cluster of specialized tubercles located between the ommatophores, occurs in some, but not all, Neotropical and Australian species; its absence apparently correlates with the presence of sympatric species. Not mentioned is the fact that a similar (homologous?) structure occurs widely in Bradybaenidae (cf. Takeda, 1982, The Veliger 24:328-330). Clearly, the real work of reckoning systematic relationships still lies ahead.

The fact that the greatest descriptive land malacologist of this century put his stamp on the Red Centre should not deter future investigators. As he himself wrote, "the present survey of Red Centre camaenids also is a first approximation. There are many obvious collecting gaps. New taxa can be found by all who use this volume to find hills or rock exposures where people have not yet looked for land snails—and go there" (p. 985). Given those collecting gaps, and the need to subject the existing data to phylogenetic analysis, there is no need, and no excuse, for a "monographic hush" to fall over the Camaenidae of Western and central Australia.

B. Roth

Bivalved Seashells of the Red Sea

by P. GRAHAM OLIVER. 1992. Cardiff (National Museum of Wales) & Wiesbaden (Hemmen). 330 pp., 46 color

plates, many text figures. Published with the assistance of British Petroleum.

Bivalves of Australia, Vol. I

by KEVIN LAMPRELL & THORA WHITEHEAD. 1992. Bathurst, New South Wales (Crawford House). xiii + 182 pp., 77 color plates.

It is gratifying that the Bivalvia are now receiving the attention they have so long deserved.

Bivalved Seashells of the Red Sea by malacological professional P. Graham Oliver covers the fauna of the corner of the Indo-Pacific province that extends into the Red Sea. The color plates are excellent, and the keys to the species are among the best ever produced.

Bivalves of Australia, Vol. I by amateurs Kevin Lamprell and Thora Whitehead covers selected families of the enormous Australian fauna, which includes not only the Indo-Pacific province on the north, but the rest of that continent's coasts as well. The volume covers the Glycymerididae, Pinnidae, Propeamussiidae, Pectinidae, Placunidae, Limidae, Trigoniidae, Lucinidae, Fimbriidae, Chamidae, Carditidae, Crassatellidae, Cardiidae, Hemidonacidae, Tridacnidae, Mactridae, Mesodesmatidae, Tellinidae, Donacidae, Psammobiidae, Semelidae, Solecurtidae, Trapeziidae, Glossidae, Veneridae, and Petricolidae. A second volume to treat other families is in progress. The authors have sought the advice of a number of specialists on various groups and have thus avoided many potential pitfalls. The plates are of good quality, but the views of small specimens suffer from having been printed at too low a magnification.

E. V. Coan

Harmful Non-Indigenous Species in the United States

U.S. Congress, Office of Technology Assessment, OTA-F-565. September 1993. U.S. Government Printing Office, Washington, D.C. 391 pp. + separately bound Summary, 57 pp. \$21.00.

Species found beyond their natural ranges "are part and parcel of the U.S. landscape. Many are highly beneficial. . . . A large number, however, cause significant economic, environmental, and health damage" (from the Foreword). This work takes a broad look at the damaging species and sets forth major policy issues and congressional options that emerged from a recent OTA analysis. References to non-indigenous mollusks and the consequences of their introduction are spread throughout the book, and listed in one place in a taxonomic index, pp. 374-375.

Predictably, the most text is devoted to the zebra mussel

(*Dreissena polymorpha* and congeners), which is projected to account for over three billion dollars in economic losses over an unspecified future span of years. Hawaii and Florida are treated as special case studies. Forty of a total of 140 land snail species in Florida are considered to be established non-indigenous species (p. 257), the highest percentage for any animal group considered.

Much of the biological information is abstracted and summarized from studies performed for the OTA by various contractors. (Not without some losses in translation; for example, the land snail *Alcadia striata* shows up identified as a clam [p. 104].) The information in these underlying reports might be of considerable use if it were made public as well, perhaps on one of the numerous freely accessible electronic mail sites that now dot the network.

The book may be ordered from the Superintendent of Documents, U.S. Government Printing Office, P.O. Box 371954, Pittsburgh, PA 15250-7954.

B. Roth

Taxonomic Revision of the Family Psammobiidae (Bivalvia: Tellinoidea) in the Australian and New Zealand Region

by RICHARD C. WILLAN. 1993. Records of the Australian Museum, Supplement No. 18. 132 pp., 416 figures.

The Psammobiidae, like many other molluscan families, reaches its greatest diversity in the Indo-Pacific realm. This monograph is based on a careful search for type material in various European museums, review of large amounts of material, and careful evaluation of some 40 shell characters. Most of the species covered are widespread in the Indo-Pacific, with the rest endemic to Australia or New Zealand. Extensive synonymies of the species are provided, together with keys, full shell descriptions, comparisons among the species, information about habitat and distribution, photographs, and line drawings.

One species each of *Asaphis* and *Heteroglypta*, 27 of *Gari* and eight of *Soletellina* are covered. Several species are excluded from the family, with most reassigned to the Tellinidae. The subfamily Sanguinolariinae is claimed to possess no unique characters and is relegated to synonymy.

The author claims (p. 5), "It seems impossible to find a set of unique, derived conchological characters . . . that unequivocally delineate the Psammobiidae." However, with few exceptions the justification for regarding any given character-state as derived or primitive is not presented. The polarity of character-state transformations is rarely argued in terms of outgroup comparison or any other criterion. Again, Willan states (p. 11), "I rank these subunits [of *Gari*] at the level of subgenera using Hennigian principles, ie, the possession of a set of unique derived char-

acters (apomorphies) by all species of a particular group.” This sentence seems to mix the two activities of grouping and assigning rank. (With respect to ranking, Hennig [1966, *Phylogenetic Systematics*. Urbana: Univ. Illinois Press] advocated that alternate branches of a dichotomy on a cladogram should be treated as of equal categoric rank; but a current trend in phylogenetic systematics de-emphasizes formal ranks.) In any case, the analytical underpinning—what are the sister-group relations among the taxa? which states of the characters are derived?—is not made explicit. Taxonomic decisions seem to have been based largely on “magnitude of difference” criteria (e.g., on p. 68, the proposal of the new subgenus *Crassulobia*) rather than on the distribution of apomorphies among the array of taxa considered.

A competent work in the mold of traditional systematics does not benefit from attempts to drape itself in the trappings of cladistic analysis. This otherwise excellent mono-

graph is not unique among recent molluscan systematic papers that “talk the talk” but do not “walk the walk” of phylogenetic systematics. In some cases the fault may be in the review process, where a reviewer, instead of granting the work the terms of its own methodology, returns the manuscript with a comment like “where are the apomorphies?” The author’s path of least resistance may then be to add a few words from the vocabulary of cladistics. (The author informs me that such was not the case in this work.) But traditional systematics and real phylogenetic systematics are different beasts; better to assign them to their own pens.

The price of the monograph is \$A30.00 bought at the Australian Museum, \$A36.00 posted economy air to other countries.

B. Roth

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Manuscripts must be typed, one side only, on A4 or equivalent (e.g., 8½" × 11") white paper, and double-spaced throughout, including references, figure legends, footnotes, and tables. All margins should be at least 25 mm wide. Text should be ragged right (i.e., not full justified). Avoid hyphenating words at the right margin. Manuscripts, including figures, should be submitted in triplicate. The first mention in the text of the scientific name of a species should be accompanied by the taxonomic authority, including the year, if possible. Underline scientific names and other words to be printed in italics; no other manipulation of type faces is necessary on the manuscript. Metric and Celsius units are to be used. For aspects of style not addressed here, please see a recent issue of the journal.

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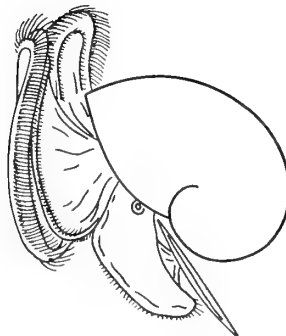
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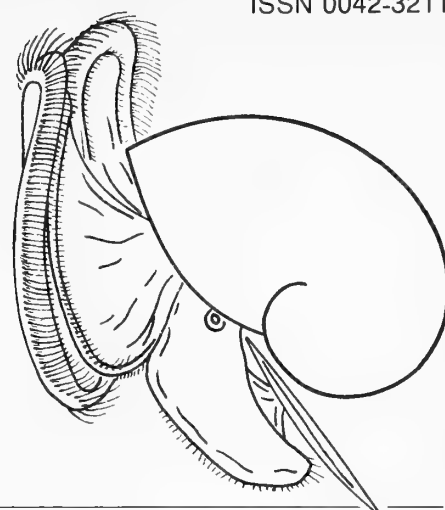
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THE VELIGER

A Quarterly published by
CALIFORNIA MALACOOLOGICAL SOCIETY, INC.
Berkeley, California
R. Stohler, Founding Editor



Volume 37

October 3, 1994

Number 4

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The Veliger (ISSN 0042-3211) is published quarterly on the first day of January, April, July, and October. Rates for Volume 37 are \$32.00 for affiliate members (including domestic mailing charges) and \$60.00 for libraries and nonmembers (including domestic mailing charges). For subscriptions sent to Canada and Mexico, add US \$4.00; for subscriptions sent to addresses outside of North America, add US \$8.00, which includes air-expedited delivery. Further membership and subscription information appears on the inside cover. The Veliger is published by the California Malacozoological Society, Inc., % Santa Barbara Museum of Natural History, 2559 Puesta del Sol Road, Santa Barbara, CA 93105. Second Class postage paid at Berkeley, CA and additional mailing offices. POSTMASTER: Send address changes to The Veliger, Santa Barbara Museum of Natural History, 2559 Puesta del Sol Road, Santa Barbara, CA 93105.

THE VELIGER

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The Veliger is an international, peer-reviewed scientific quarterly published by the California Malacozoological Society, a non-profit educational organization. *The Veliger* is open to original papers pertaining to any problem connected with mollusks. Manuscripts are considered on the understanding that their contents have not appeared, or will not appear, elsewhere in substantially the same or abbreviated form. Holotypes of new species must be deposited in a recognized public museum, with catalogue numbers provided. Even for non-taxonomic papers, placement of voucher specimens in a museum is strongly encouraged and may be required.

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Two New Species of Eulimid Gastropods Endoparasitic in Asteroids

by

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AND

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Abstract. Two new species of the genus *Asterophila* Randall & Heath, 1912 (Prosobranchia, Eulimidae) are described, *A. perknasteri* from the Antarctic starfish *Perknaster* sp. (Valvatida, Ganeriidae) and *A. rathbunasteri* from the californian starfish *Rathbunaster californicus* Fischer, 1906 (Forcipulatida, Asteriidae). A third species of *Asterophila* is reported from *Freyella* sp. (Brisingida, Brisingidae), from the southern part of the Kermadec Trench, but is not described.

INTRODUCTION

The family Eulimidae consists of gastropods parasitic on and in echinoderms. Most species are temporary ectoparasites that spend most of their time hiding in bottom sediment, occasionally taking a meal from a nearby, suitable echinoderm. Such species maintain most of the normal gastropod anatomy. Other species are highly modified endoparasites that spend most of their lives attached inside the host specimen, having only a short free-swimming larval stage during which they find new host specimens. Warén (1984) presented a list of the genera and what was known about the biology of the species of Eulimidae.

Here we describe two new species of *Asterophila* and summarize the present knowledge on the genus, which previously was not easily accessible since it was published in Russian.

MATERIALS AND METHODS

This paper is based on specimens forwarded to Warén from various surveys. The specimens are enumerated under each species, together with the location of the material.

For the description of the parasites and the method of parasitism, the arms of the starfishes were opened cautiously, starting some distance away from the swellings to avoid damaging the parasites. Photographs of selected snails

in situ were taken using WILD M420 macrophoto equipment. A few specimens were stained with karm-alum to contrast the organs of the very pale and featureless bodies. To illustrate certain features, some specimens were critical point dried via acetone and carbon dioxide and photographed with a scanning electron microscope (SEM).

SYSTEMATICS AND DESCRIPTIONS

Gastropoda, Prosobranchia,
Neotaenioglossa

Family EULIMIDAE Philippi, 1842

Asterophila Randall & Heath, 1912

Type species. *Asterophila japonica* Randall & Heath, 1912, by original designation. Parasitic in *Pedicellaster magister orientalis* Fischer, 1928 (Forcipulatida: family Pedicellasteridae) from Japan.

Remarks: Randall & Heath's (1912) description of *Asterophila* is not very detailed, and Grusov's (1965) excellent redescription is in Russian. Therefore we present here a rather detailed introduction to the genus, supplemented by our observations. Until the present time, *Asterophila* has contained only the type species.

Grusov (1965) redescribed *Asterophila japonica* in great

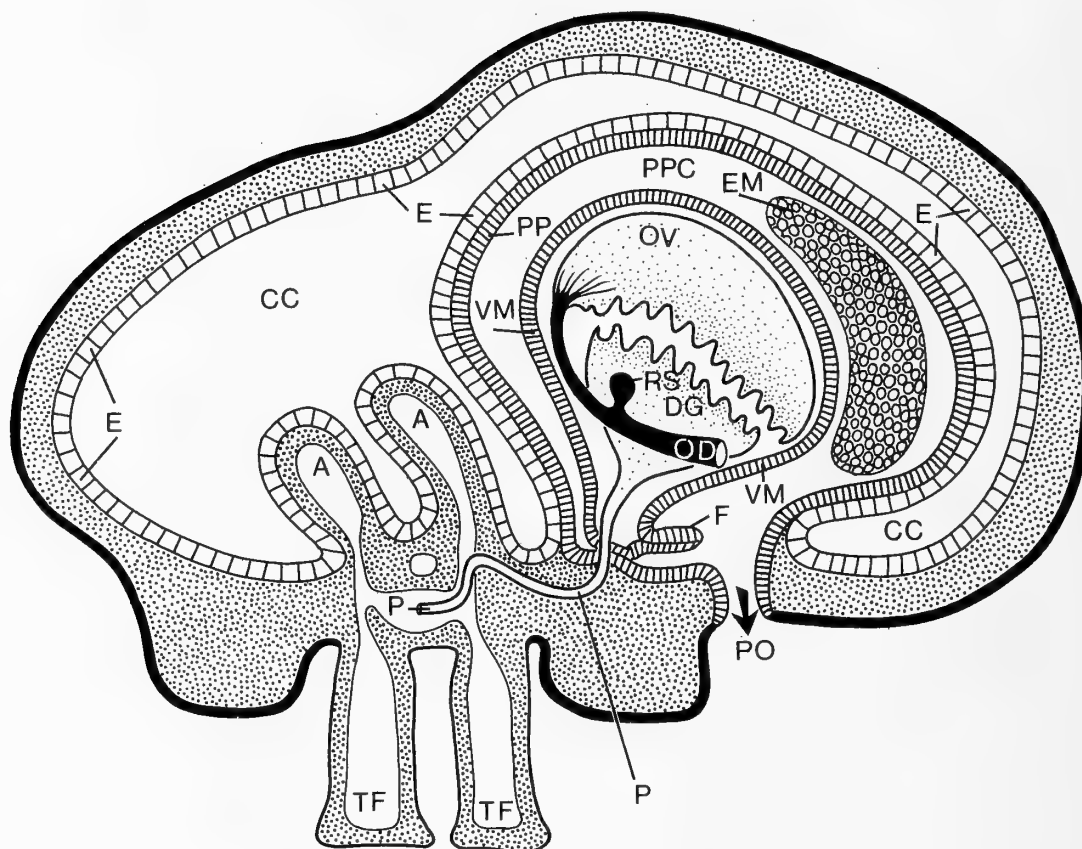


Figure 1

Schematic cross section of an arm of a starfish with *Asterophila* sp. in its body wall (and cavity). The snail has caused an abnormal swelling of the right half of the arm. It is surrounded by the pseudopallium, has a proboscis leading to the radial canal, and its pseudopallial cavity opens to the exterior via a pore, where an arrow marks the assumed exit path for the larvae.

A—ampullae; CC—coelomic cavity of the starfish; DG—diges-

tive gland; E—coelomic epithelium of the starfish; EM—egg mass of the snail in the pseudopallial cavity; F—foot of the snail; OD—glandular oviduct; OV—ovary of the snail; P—proboscis; PO—pore from the pseudopallial cavity; PP—pseudopallium; PPC—pseudopallial cavity; RS—receptaculum seminis; TF—tube foot of the starfish; VM—visceral mass.

detail, based on 600 specimens, several of which were serially sectioned. He recorded *A. japonica* from the Bering Strait to Korea, in 14–700 m depth from several host species: *Ctenodiscus crispatus* (Retzius, 1805) (Paxillosida: family Gonioplectinidae); *Leptychaster* sp. (Paxillosida: family Astropectenidae); *Cribrella* sp. (= *Henricia* sp.) (Spinulosida: family Echinasteridae); *Leptasterias polaris* (Müller & Troschel, 1842); *L. groenlandica* (Lütken, 1857); and *L. arctica* (Murdoch, 1885) (Forcipulatida: family Asteroiidae).

External examination by the senior author of several hundred specimens of *Ctenodiscus crispatus* from Svalbard and northern Norway in the extensive collections of the Swedish Museum of Natural History, gave no reason to suspect its presence there.

Hoberg et al. (1980) found *Asterophila japonica* in the northeastern Bering and Chukchi Seas, in *Leptasterias arc-*

tica and *L. polaris acervata* (Stimpson, 1862), and reported a prevalence between 2 and 60 percent. It is thus known from most of the orders of asteroids. This is unusual for eulimid gastropods, which usually are quite and sometimes very host specific (Warén, 1984). Usually the endoparasitic and permanently attached species exhibit a higher specificity than those that regularly leave the host, which makes this wide range of hosts more surprising.

Stone & Moyse (1985:1270) reported an endoparasitic gastropod from the deep-sea asteroid *Freyella* sp. living in the same specimens as an ascothoracid crustacean, but did not suggest its identity. Examination of the specimens, kindly sent for examination, showed that they belong to *Asterophila*, and they are briefly described (but not named) below. So far no other distributional information has been published on the genus.

Asterophila is a highly modified gastropod, and Figure

1 is a schematic representation of the organization and the position of the female in the host. The male is much smaller than the female, being less than one-tenth of her size. The male is either attached to the pseudopallium of the female or lives in her oviduct.

Young specimens are assumed to start their lives in the body wall of the asteroid, but as they grow, they force the coelomic epithelium to bulge into the coelomic cavity, so that the parasite ends up lying in the cavity, completely covered by the coelomic epithelium. Frequently, one or several ampullae of the tube feet, or other organs of the host, are included in the external cover formed by the coelomic epithelium.

The head and parts of the proboscis (cf. below) of the snail are modified into a large balloonlike wrapping which covers the visceral mass (the so-called pseudopallium) and leaves a large space between the visceral mass and the pseudopallium. Mature specimens use this space for storing the large egg mass which is contained by a thin membrane and is partly wrapped around the visceral mass.

It was not mentioned by Grusov (1965), but judging from the presence of rudimentary tentacles on the inside of the pseudopallium of *A. perknasteri*, the head of the snail contributes to the formation of the pseudopallium. These small bulges were verified as tentacles by following the large nerves which innervate them and which connect directly to the cerebral ganglia. These nerves were mentioned by Grusov (1965:fig. 31, number 13, dorsal pair) together with two more ventral pairs, all called "pseudopallial nerves." The dorsal pair corresponds in position to tentacle nerves in other eulimids, while the two more ventral pairs seem to correspond to the nerves innervating the proboscis sheath ("snout" in Grusov 1965; the real snout is lost or transformed into the proboscis sheath in the least modified eulimids). In the following descriptions, the term "stalk" is used for this part of the snail, formed by the head-foot and constituting a connection between the pseudopallium and the visceral mass. On the stalk can be seen the rudimentary foot. The stalk also contains the central nervous system.

The presence of the rudimentary tentacles facilitates the orientation of the specimens by defining the front of the animal. Posterior to the stalk is a pore through the pseudopallium. This part of the pseudopallium is thickened, more muscular and bulges into the body wall of the host, where it usually causes deformation of the skeletal elements. Frequently there is also a corresponding pore in the body wall of the host, and the pseudopallial cavity is thus in communication with the surrounding sea.

In the center of the stalk runs the esophagus. Distally to the pseudopallium the esophagus continues inside the proboscis sheath, which also is formed by the hypertrophied tissues around the "real" mouth. At the same time, the esophagus is elongated so that the real mouth is situated at the end of the proboscis sheath. *Asterophila perknasteri* and *A. rathbunasteri* can retract at least parts of the proboscis into the stalk.

Asterophila japonica has a very short, sometimes almost non-existent proboscis (Grusov, 1965), but in *A. perknasteri*, the proboscis may be as long as the diameter of the body (when leading to the subradial canal, in small specimens even three times the body diameter), while in specimens attached close to the gonad, it may be very short. This discrepancy between *A. japonica* and *perknasteri* may have been caused by the fact that specimens of the former species, with a long proboscis, had been damaged when removed from the host and/or that Grusov's observations of the proboscis were based on specimens with an unusually short proboscis. We find it likely that the length of the proboscis to some extent is individually adjusted by growth (since there are no internal retractors; Grusov, 1965:127) to the position of the snail in relation to suitable food sources.

The snails are assumed to feed by pumping body fluid from the host, usually from the subradial canal. This fluid is taken directly into the digestive gland, which is covered by the gonad.

Both large and small specimens have a well-developed pseudopallial pore forming a communication to the surrounding sea. Possibly this gives some clues about its evolutionary origin and function: It may be a rudiment of an evolutionary sequence, from shell-bearing ancestors sitting in a bowl-shaped depression in the external body wall of the host; and its present function in recently settled specimens may be to allow a larva to enter through this pore to become its mate. The presence of remains of one or two larval shells in the pallial slit of several small females of *A. perknasteri* with no egg mass or an egg mass in an early stage of development, supports this hypothesis.

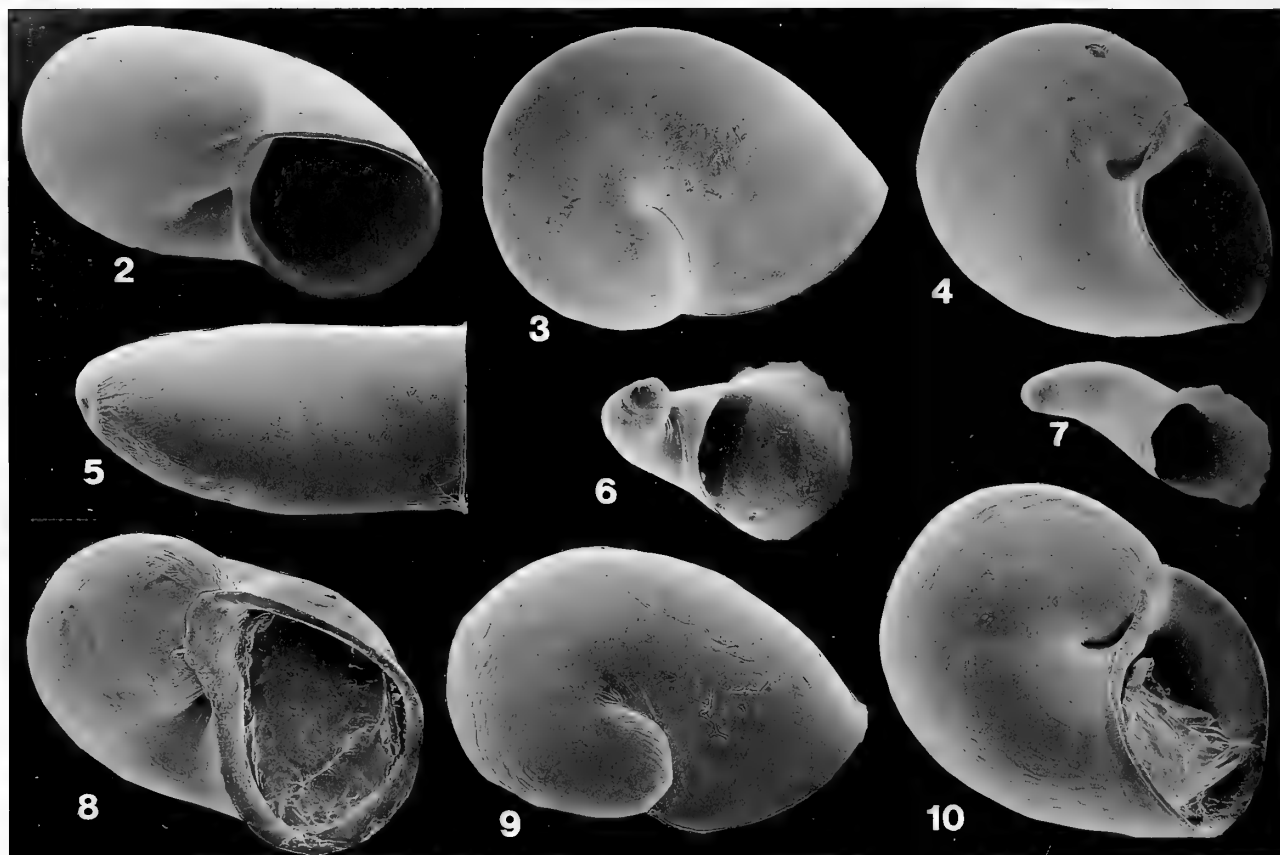
Small specimens, one-eighth to one-fourth of maximum size, have no egg mass, but larger specimens usually have one.

Many specimens of *A. perknasteri* and *A. rathbunasteri* with newly laid eggs in the capsule had a virtually empty visceral mass, which together with the fact that all eggs in an egg capsule are in the same stage of development, suggests that egg laying takes place during a short time. Other specimens with a large capsule full of seemingly mature veliger larvae had filled their visceral mass again with stored nutrients, suggesting preparations for the next spawning.

Nothing is known about the life span of the parasites, except that they evidently produce more than one brood of eggs.

Egg masses of mature specimens may contain from many hundreds in the smallest specimens up to several tens of thousands of eggs or developing embryos (in large specimens of *A. perknasteri*), and is evidently directly related to the body volume.

The larval shell (protoconch 1), which does not grow between the late larval stages in the egg capsule, and the empty larval shells found inside females of *A. perknasteri*, indicates lecithotrophic development. The morphology of the larvae (see Grusov, 1965) indicates that they have a



Explanation of Figures 2 to 10

Larval shells of *Asterophila* spp.

Figures 2–4. *A. perknasteri* Warén, sp. nov., diameters 690, 720, and 710 μm .

Figure 5. *A. rathbunasteri* Warén, sp. nov., abnormal larval shell, length 610 μm .

Figures 6, 7. *A. perknasteri* Warén, sp. nov., abnormal larval shells, length 690 and 900 μm .

Figures 8–10. *A. rathbunasteri* Warén, sp. nov., diameters 480, 515, and 500 μm respectively.

free-swimming dispersal stage, enabling them to find new hosts.

The youngest larvae with a shell are about two-thirds of the size of the mature larvae, and their shell includes only the first part of the final protoconch. Such larvae have a large and solid digestive gland, which evidently stores

nutrition and supplies material for further growth, since the digestive gland is smaller and less dense in the largest larvae. In each egg mass, the stage of development and size of the larvae are very uniform, except for scattered abnormal larvae (Figures 5–7). Such larvae are rare, occurring only in scattered females, but then usually several

Explanation of Figures 11 to 13

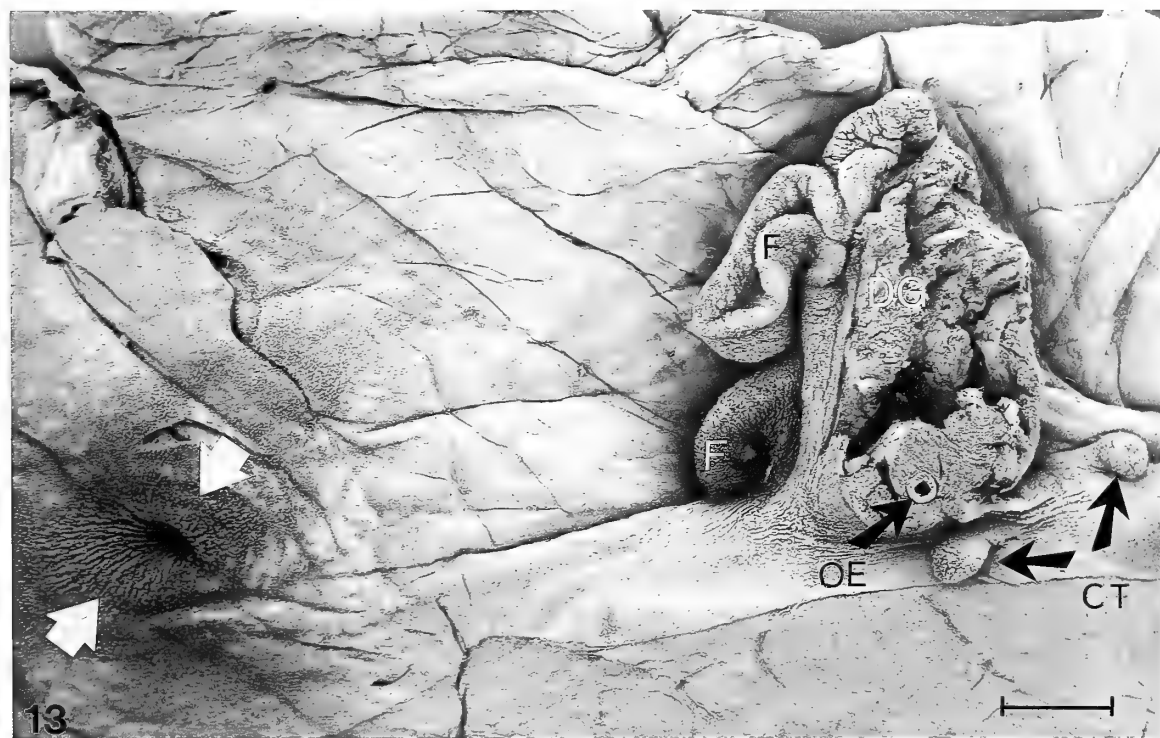
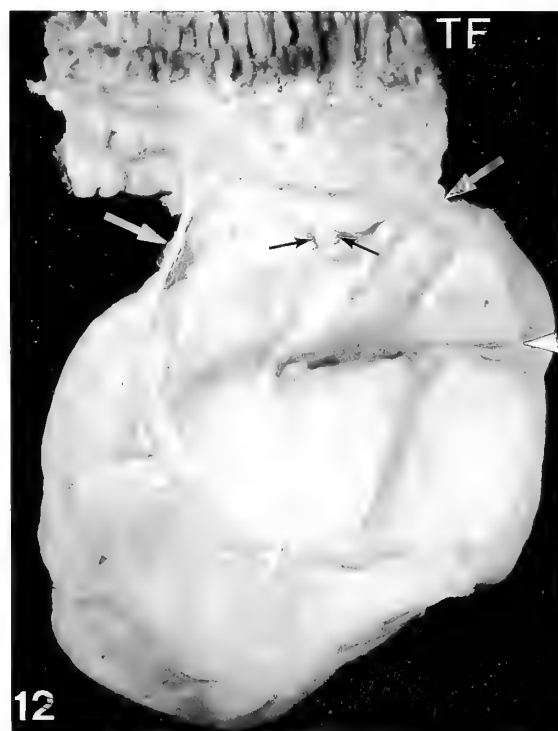
Asterophila perknasteri Warén, sp. nov.

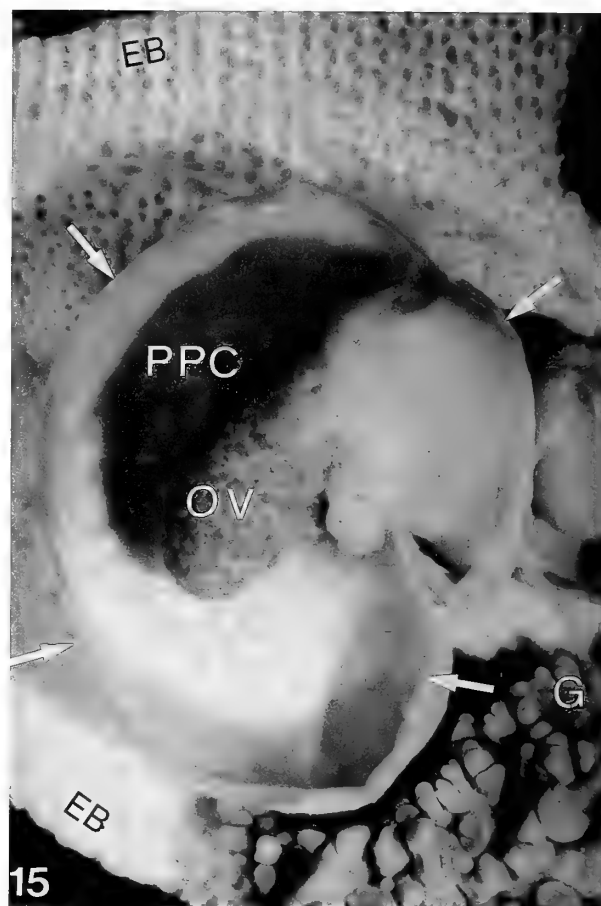
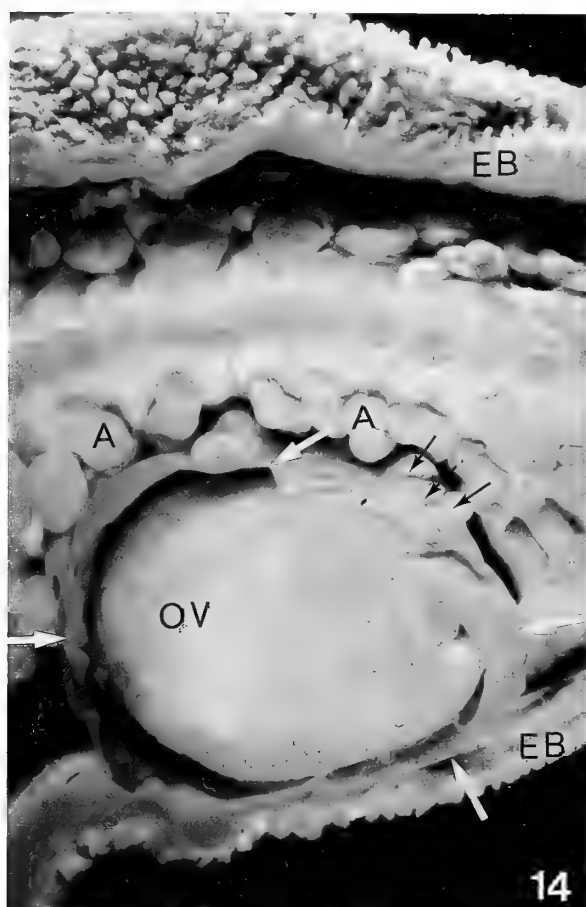
Figure 11. Piece of an arm of *Perknaster* sp., external view of the pore connecting to the pseudopallial cavity of the snail (indicated by two arrows). Scale line 3 mm.

Figure 12. Holotype, intact with a piece of the arm of the host. Maximum diameter of cyst ca. 30 mm. Coelomic epithelium of the host opened and indicated by white arrows. Proboscis indicated by two thin, black arrows.

Figure 13. Interior of the pseudopallial cavity of *A. perknasteri* Warén, sp. nov., showing the exit pore (marked with arrows) and stalk of the snail. The visceral mass has been removed to show the rudiments of the foot and the tentacles. Scale line 2 mm.

CT—cephalic tentacle; F—foot; OE—esophagus; DG—digestive gland; TF—tube foot.





Explanation of Figures 14 and 15

Asterophila perknasteri Warén, sp. nov. in *Perknaster* sp., from *Proantar*.

Figure 14. Specimen attached laterally on the ambulacrum. Pseudopallium (indicated with white arrows) opened to show the visceral mass of a specimen without an egg mass, presumably ready to form one. Some ampullae of the host (marked by black arrows) have been incorporated with the coelomic epithelium on the pseudopallium. Diameter of cyst 12 mm.

Figure 15. Specimen attached to the aboral body wall of host, close to the disc. The pseudopallium has been opened and egg mass removed to show the much smaller size of the visceral mass soon after spawning. Diameter of cyst 15 mm. A second much smaller specimen is visible at the right edge of the picture.

A—ampullae; OV—ovary of the snail; G—gonad of the host; PPC—pseudopallial cavity; EB—external body wall of the host.

deformed larvae. The uniformity in the development indicates that spawning is not continuous but takes place during a short time.

The size and structure of the larval shell is very uniform in the egg masses which have been examined within one host species: Mature stages of *A. rathbunasteri* measure 460–520 μm in maximum diameter and in *A. perknasteri* 650–750 μm . The size thus seems to differ between species, and can be used for species identification in these cases. Hoberg et al. (1980) reported an average size of the larvae of 0.48 mm (range 0.28–0.60 mm) in *A. japonica*. Grusov (1965:fig. 44) figured larvae with a maximum diameter of

0.36 mm, but mentioned a maximum diameter of the larvae of 0.57 mm (the same sizes given by Grusov, 1966:177). The large variation indicates that these figures probably include young larvae, and cannot therefore be used for comparison between different species.

Specific identification of species of *Asterophila* is difficult since the species have few comparable characters and usually are quite distorted by the contractions of the host asteroid when it was preserved. It seems also that the posterior part of the foot (when it is present) and the rudimentary appendages of the head and their position are quite variable.

Asterophila perknasteri
Warén, sp. nov.

Figures 2–4, 6–7, 11–15

Type locality: Antarctica, western coast of Graham land, *Hero* Cruise 824, station 24–1, 64°15.2'–64° 14.5'S, 61°27.5'–61°25.9'W, 540–605 m, in three *Perknaster* sp. (Valvatida: family Ganeriidae) with 6–8 parasites each. Collected by J. E. Dearborn and G. Hendler.

Type material: Holotype USNM 8603370 (Figure 12). Six lots in alcohol, from the type locality, each with one or several gastropods, plus one sample of dried and one of wet larval shells are all considered paratypes, USNM 8603371–8603377. Reference material of the host starfish is kept at the collection of echinoderms, USNM E43012.

Material examined: The type material and: *Proantar IV*, 02 February 1986, station 4865, 62°55.0'S, 55°16.5'W, 82 depth m, Antarctica, north of Joinville Island and north-east of Palmer Peninsula. 3 *Perknaster* sp. with many *Asterophila*. *Proantar IV*, 02 February 1986, station 4874, 63°25.8'S, 62°19.8'W, 135 m, 14 February 1986. Just southwest of South Shetland Islands. 2 *Perknaster* sp. with 4 *Asterophila*. *Proantar IV*, 02 February 1986, station 4875, 63°17.4'S, 62°30.2'W, 157 m, 14 February 1986. Just southwest of South Shetland Islands. 1 *Perknaster* sp. with 1 *Asterophila*. The specimens above were collected during the "Programa Antártico Brasileiro" (*Proantar*), during work carried out from "N.Oc. Prof. W. Besnard," and the specimens were forwarded by L. de Siqueira Campos. This material is now kept at the Oceanographic Institute of the University of Sao Paulo.

Description: The cysts (Figure 12, 14–15) are large, up to 30 mm diameter of the pseudopallium. They are situated in a large blister between the body wall and coelomic epithelium of the host, bulging into and partly filling the coelomic cavity of the arms. The proboscis leaves the pseudopallium and runs just under the coelomic epithelium, usually toward the ambulacrum, enters a tube foot and continues via this to the subradial canal. In dorsally attached specimens, the proboscis runs for a long distance through the body wall, but it was not possible to find its end in such specimens. On the inside of the pseudopallium, a few millimeters from the stalk, two conspicuous small bulges represent the cephalic tentacles (Figure 13:CT). Some distance behind the stalk and somewhat to the right is a pore in a thickened part of the pseudopallium (Figure 13: white arrows), usually corresponding to a bowl-shaped impression in the body wall of the host. This impression sometimes has a pore opening externally on the body wall of the host (Figure 11). The thickened part of the pseudopallium is evidently muscular, since it has a system of concentric and radial ridges surrounding the opening. The rudimentary and distorted foot (Figure 13:F) is situated on the right side at the transition from the stalk to the

visceral mass. Its anterior part is tonguelike and free. The posterior part has a poorly defined system of furrows and folds, perhaps also involving opercular lobes. At the anterior right side of the stalk, one specimen has a triangular process, possibly a rudimentary penis. Some specimens have additional little bumps at the anterior part of the stalk, possibly additional cephalic tentacles. The right corner of the pallial cavity is swollen and solid, and seems to be a partly evaginated pallial oviduct. Above the left part of this swelling starts a furrow which continues clockwise all around the stalk and joins itself above the posterior part of the swelling. This is the pallial margin. The pallial oviduct opens just inside the pallial cavity central to the swelling, but no groove could be traced from here to carry the eggs away. The basal third of the visceral sack contains the poorly discernable pericardium and kidney plus the digestive gland; the apical part contains the large gonad.

The egg mass is contained within a thin membrane which in turn is stuck to the visceral mass (but not to the pseudopallium) and has a volume up to twice that of the visceral mass. It is stored in the pseudopallial cavity apically and around the visceral mass. Large specimens have an egg mass containing more than 40,000 embryos or larvae. The average egg diameter is about 300 μm , and the final size of the larval shell (Figures 2–4) is about $720 \times 500 \times 400 \mu\text{m}$. Examination of several thousand larvae of *A. perknasteri* from many females and measurements of all that were extra large or small showed a range of 650–760 μm .

The male was not found, but several small females with no egg mass or an egg mass containing only early cleavage stages had one or two empty larval shells (usually partly dissolved or resorbed) stuck in the pallial slit, and it is assumed that the male is attached in the pallial cavity or inside the oviduct. The smallest ovigerous female was 2.8 mm in maximum diameter of the pseudopallium.

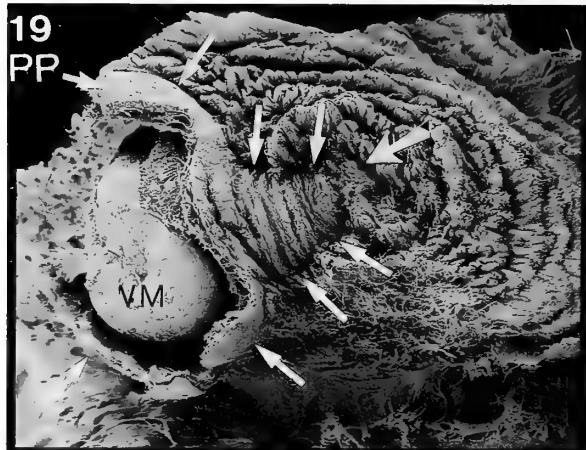
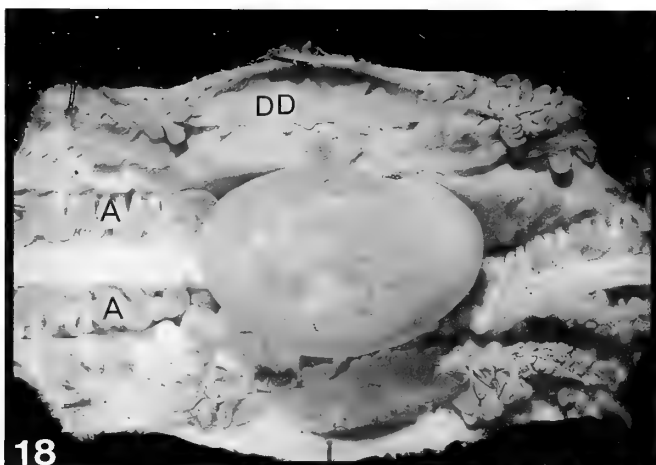
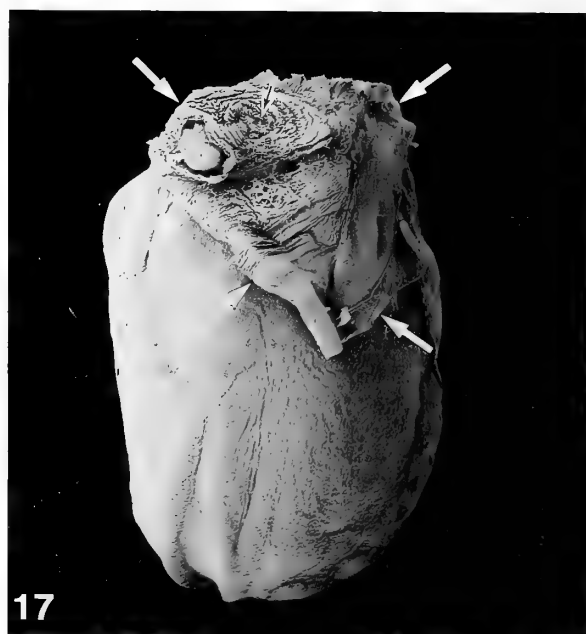
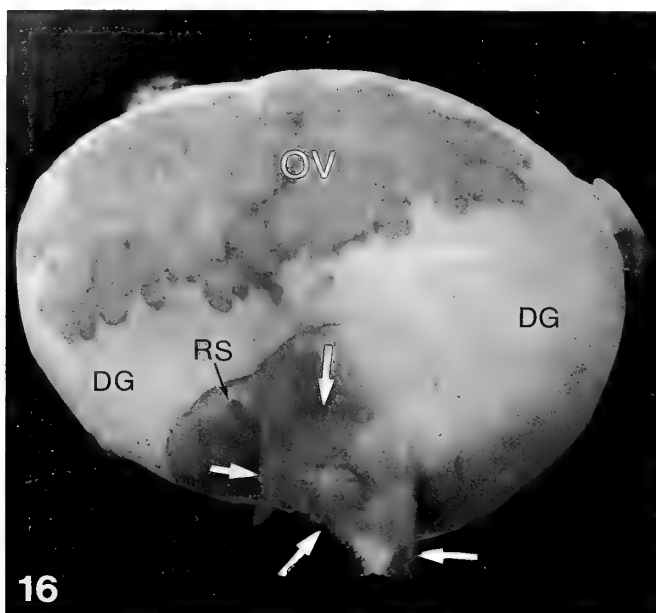
Remarks: The gross organization of *A. japonica* and the specimens above is similar in most features, but the detailed anatomy of the reproductive system remains to be compared. This would have required serial sectioning of a couple of mature specimens, work we did not consider necessary to diagnose the present species.

The presence of empty larval shells, the absence of an externally visible receptaculum seminis, and absence of externally situated males seems enough evidence to assume that the males are internal in the female and probably living parasitically in her oviduct.

A comparison with *Asterophila japonica* shows the following differences:

1. *Asterophila japonica* has one or several males attached externally on the pseudopallium, close to the pseudopallial pore, while we presume *A. perknasteri* to have internal males.

2. *Asterophila japonica* has larvae of a maximum diameter of about 600 μm , while those of *A. perknasteri* are



Explanation of Figures 16 to 19

Asterophila rathbunasteri Warén, sp. nov.

Figure 16. Visceral mass, weakly stained with karm-alum. The pseudopallium has been removed, except a small area around the stalk, marked with white arrows. The two top and left of these are placed on the darkly staining pallial oviduct, where the receptaculum seminis just barely can be seen. Maximum diameter of visceral mass 12 mm.

Figures 17, 19. Critical point dried female with its dwarf male. Most of the pseudopallium has been removed, the remaining part indicated by white arrows. The shorter black and white arrow

indicates the pseudopallial pore. 19. Detail of Figure 18, showing exterior of pseudopallium with a male (demarcated by white arrows) and the pore (marked by a larger arrow). The pseudopallium of the male has been opened to expose the visceral mass.

Figure 18. Intact holotype in arm of *Rathbunaster californicus*. Length of cyst 13.5 mm.

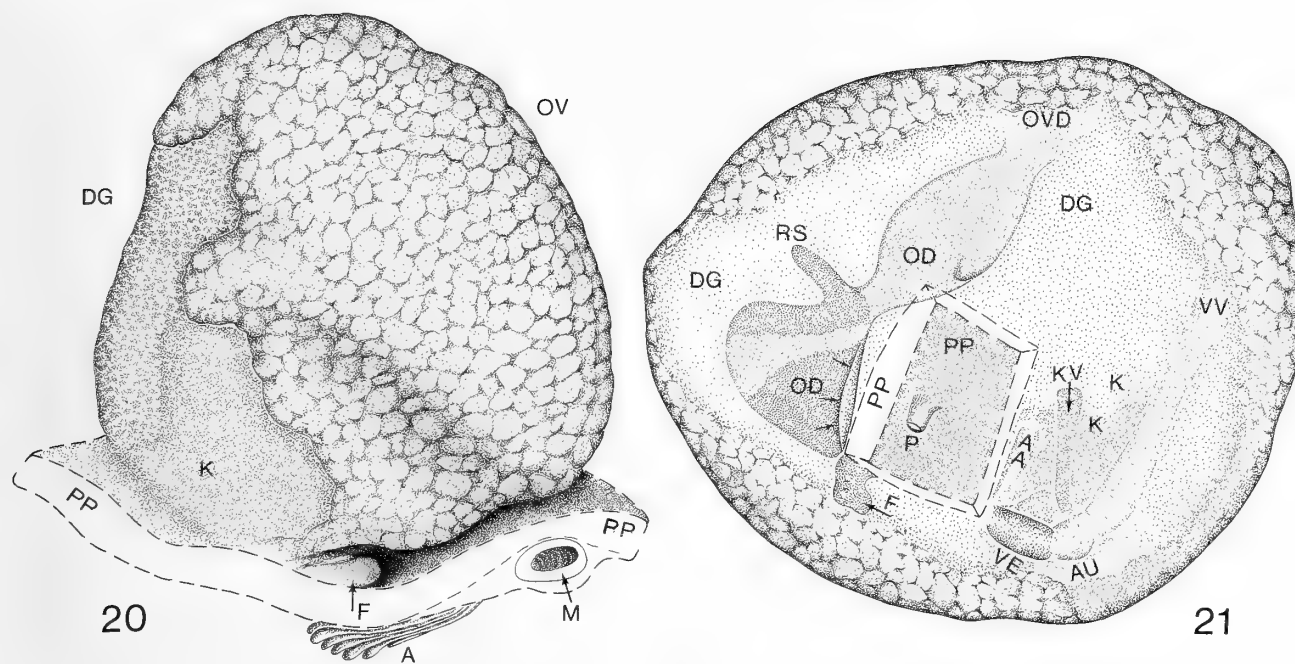
A—ampullae; DD—digestive diverticulae of starfish; DG—digestive gland; OV—ovary; PP—pseudopallium; VM—visceral mass; RS—receptaculum seminis.

about 650–760 μm . Furthermore, the ratio between the largest and smallest diameter of the larval shell is 1.8 in *A. japonica* but 1.5 in *A. perknasteri*.

3. Grusov (1965) did not mention the presence of rudimentary tentacles in *A. japonica*, nor are they figured in

his excellent and detailed drawings. These tentacles are conspicuous in *A. perknasteri*.

The host starfish could not be determined specifically, but if a need arises, there are voucher specimens of the host in USNM (see "Type material").



Explanation of Figures 20 and 21

Asterophila rathbunasteri Warén, sp. nov., visceral mass. The pseudopallium has been removed, except around the stalk. Diameter of both specimens ca. 5 mm.

Figure 20. Lateral view, showing the very small rudiment of the foot, the position of the male, and a strongly folded ampulla, incorporated with the coelomic epithelium around the pseudopallium.

Figure 21. "Front view," showing most of the internal organs

by transparency. The pseudopallium has been removed except for a square piece around the proboscis.

AA—anterior aorta; AU—auricle; DG—digestive gland; F—foot; K—kidney; KV—kidney vein; M—male cyst; OVD—ovarian duct; OD—glandular oviduct, opening in a narrow slit marked with 3 arrows; P—proboscis; PP—pseudopallium; RS—receptaculum seminis; VE—ventricle; VV—visceral vein.

Asterophila rathbunasteri
Warén, sp. nov.

Figures 5, 8–10, 16–21

Type material: Holotype, USNM 860366, numerous paratypes in USNM. Additional voucher material deposited in Los Angeles County Museum of Natural History.

Type locality: Off California, Monterey submarine canyon, ca. 36.5°N, 122.2°W, depth about 250–650 m. Parasitic in *Rathbunaster californicus* Fischer, 1906 (Forcipulatida, family Asteroiidae). Collected by L. Lewis and J. Nybakken, from June 1990 to November 1991.

Description: Cyst (Figure 18) globular to bean-shaped, up to 13 mm maximum diameter. The stalk is very short, with the anterior part of the foot (Figure 20:F) protruding like a small tongue, directly above the pseudopallial pore. The posterior part of foot could not be found. There are no tentacle rudiments. The pseudopallial pore (Figure 17) is small, with a thickened and ridged area around it.

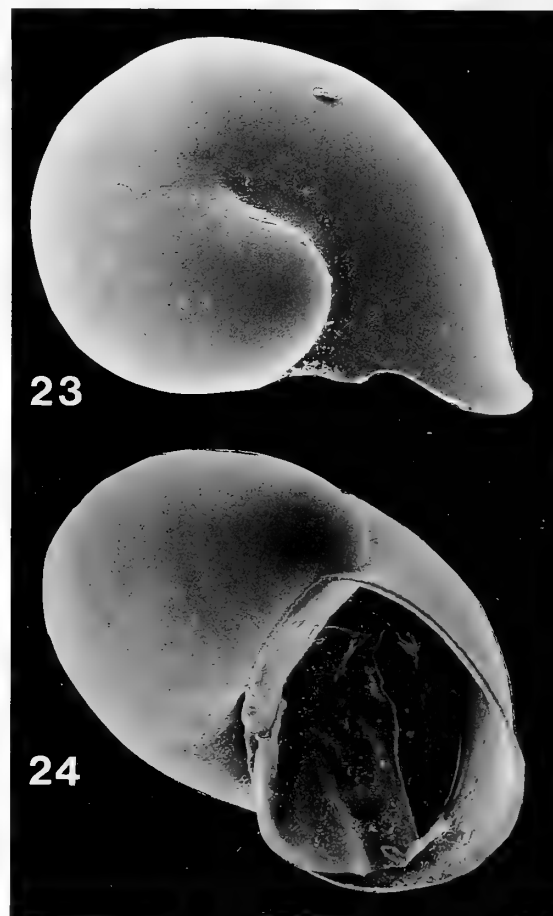
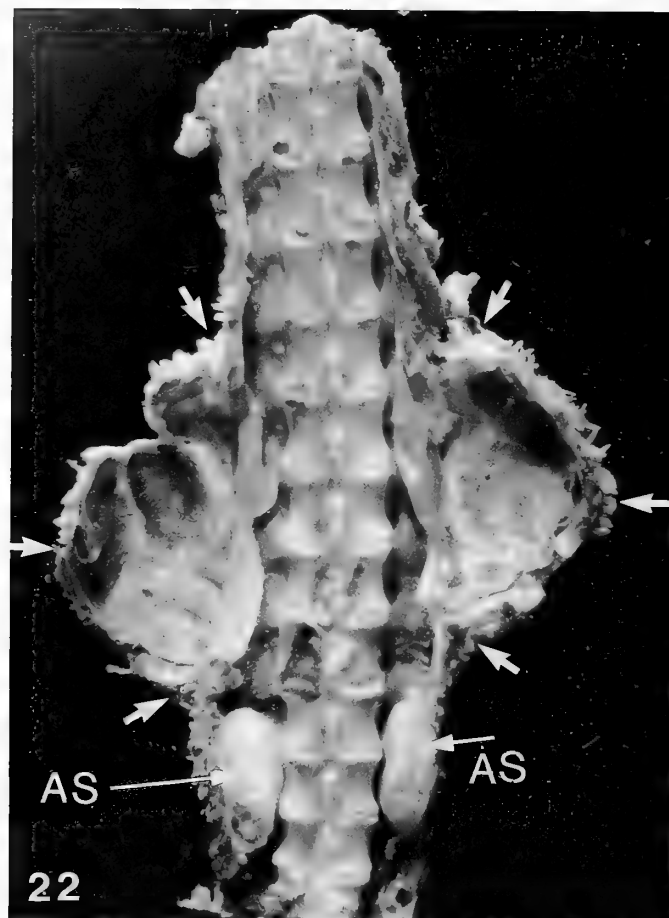
The pseudopallial pore in females with mature veligers is resting in a depression in the body wall of the host. In one specimen still *in situ*, it communicated with a duct into

a papulum (dermal gill), and could be followed with an eyebrow hair to the distal part of the papulum. This duct appeared to open through the papulum.

Juvenile specimens (cyst diameter 2–3 mm) have a more prominent pore than adults, and it is possible that the young male enters through a pore that the female has made in the skin of the host.

The oviduct (Figure 21:OD) is lying superficially and is bright, opaque, snow white. Its shape is highly variable, but usually divided into two parts by a constriction where the receptaculum seminis is situated. This is a club-shaped appendix also lying close to the body wall, directed apically at a right angle to the length axis of the oviduct. The oviduct is lying in a half circle close to the stalk. The distal part opens via a narrow slit, a vestigial pallial cavity, close to the reduced foot. Clockwise from the constricted part of the oviduct is the albumen gland, which is connected to the large ovary via a superficial and thin-walled ovarian duct.

The proboscis sheath is very short, but it is not known how much this is caused by contraction. It is muscular, and in one specimen, it was completely retracted, lying inverted into the cephalopodal haemocoel. In other spec-



Explanation of Figures 22 to 24

Asterophila sp., in *Freyella* sp.

Figure 22. Opened arm of the host starfish with cavities (demarcated by arrows) from two specimens of *Asterophila* sp. Distally (below) to these are two specimens of the ascothoracid *Bifurgaster kermadeca* (Stone) (arrows "AS"). Length of opened arm 17 mm.

Figures 23, 24. Larval shells, diameter 0.6–0.7 mm.

imens, the proboscis sheath ended at the dermal skeleton of the host, which was penetrated by a thin canal leading to the cavity of a tube foot.

The egg mass occupies most of the space in the pseudopallial cavity and is contained by a thin membrane. It contains up to about a thousand eggs or embryos. Some females have large quantities of "yolk" surrounding the embryos. The diameter of uncleaved eggs is 250–300 μm . In any one female, all larvae are in the same stage of development, but this stage can vary between different females in the same host, suggesting that there is no seasonality in reproduction, only individual periodicity.

The larvae start to form a shell (which then is extremely thin and fragile) at a diameter of about 400 μm . Mature larvae (Figures 8–10) measure 460–520 μm in diameter (largest and smallest from several females measured).

The male (Figures 17, 19) lies in a cyst in the pseudopallium, close to the pseudopallial pore, and communicates with the pore via a duct in the pseudopallium. The

body of the male consists of a visceral mass, 0.5 mm in diameter, and a rudimentary foot about 0.2 mm broad and 0.5 mm long. The duct evidently transports sperm to the pore, from where it may then be transported by the anterior part of the foot of the female which is situated close to the opening of the pallial oviduct. The inside of the male duct and the pore absorb karm-alum dye more readily, while the interior of the wall of the pseudopallium hardly absorbs it at all. This is a good indication that some activity unusual for the pseudopallium takes place there.

Remarks: *Rathbunaster californicus* is a large asteroiid starfish with 8–22 arms. It is known from the American west coast, from southern Alaska to Monterey Bay in California, in depths between 60 and 1000 meters. It is a benthic predator and scavenger with ability to catch mobile benthopelagic prey (Carey, 1972; Lewis, unpublished thesis). Five hundred host starfishes from several sites in the Monterey Bay were examined externally to determine the local

prevalence. This was found to vary between 0 and 59 percent of the hosts. These figures are, however, too low because dissection of 50 starfishes usually doubled the rate obtained from external observation.

The number of parasites per host starfish was usually more than one at the richer localities, which means that the snail was several hundred times more common at some localities compared with the poorest ones. Up to six snails could be found in a single arm, and the maximum total weight of the snails from one host corresponded to 13.8% of the body weight of the host.

Attempts were made to determine whether the starfishes were harmed by the parasitic snail, by comparing the gonads between parasitized and unparasitized individual arms and starfishes, but no significant average difference was detected. However, gonads were missing in one arm with six snails and one arm with five snails (four and three cases, respectively, were examined). This was otherwise a rare phenomenon (Lewis, unpublished thesis).

The detailed internal organization of the visceral mass was not examined; this would have required histological sectioning. The intentions were to describe the external morphology in enough detail to allow recognition of the species.

A comparison with *Asterophila japonica* shows a single major difference: The male is lying embedded in the pseudopallial wall in *A. rathbunasteri*, attached externally in *A. japonica*. There may be other differences, e.g., in the larval shell, but that has been described too incompletely in *A. japonica* to allow comparison.

Asterophila rathbunasteri differs from *A. perknasteri* in the size of the larval shell which is 460–520 μm and completely smooth in *A. rathbunasteri*, 650–750 μm and slightly “wrinkled” in *A. perknasteri*. *Asterophila rathbunasteri* differs also by lacking rudimentary tentacles, having the male living in the pseudopallium (position not known but absent in pseudopallium in *perknasteri*), and by having a more reduced foot.

Asterophila sp.

Figures 22–24

Material examined: From *Freyella* sp. (Brisingida: family Brisingidae), southern part of the Kermadec Trench, *Galathea* Expedition, station 661, 36°07'S, 178°52'W, 5480 m depth, 23 February 1952. 3 specimens of *Asterophila* found in two hosts, in connection with work on endoparasitic ascothoracids (Crustacea), by C. Stone (Stone & Moyses, 1985). The specimens were already dissected when sent to Warén, and only scattered notes on various features could be obtained. This material is now kept in the Zoological Museum of the University of Copenhagen.

Remarks: The specimens were in poor condition, and the limited material does not allow comparison with the other species.

Two specimens were sitting in galls in the body wall,

covered by the coelomic epithelium in one arm. A single specimen in another arm was situated in the same way. The diameter varied between 4 and 7 mm. Only one of them had veliger larvae (Figures 23–24), two of which still were intact when Warén received the specimen used for SEM. They had a maximum diameter of 600–700 μm . In the arm with a single parasite, the proboscis was found, directed toward the ambulacrum. The other two galls also had holes directed toward the ambulacral system, which may have been caused by proboscides. No males were found. No tentacles were seen in the remains of the pseudopallium. The pseudopallial pore was surrounded by concentric muscular ridges and was situated apically in one specimen, laterally in the second, and had been lost during the dissection of the third.

ACKNOWLEDGMENTS

We thank Dr. Lucia de Siqueira Campos-Creasey, Department of Oceanography, Southampton, United Kingdom; Professor L. R. Tommasi, University of Sao Paulo, Brazil; Professor John H. Dearborn, University of Maine, Dr. Gordon Hendler, now at Los Angeles County Museum; and Dr. Carolyn Stone, Department of Zoology, University College of Swansea, Wales, for communicating these interesting specimens, and apologize for the long time it has taken the senior author to process them.

Dr. James Nybakken, Moss Landing Marine Laboratories, California, made some of the initial examinations of *Asterophila rathbunasteri*, and offered valuable comments on the manuscript.

C. Hammar, Stockholm, prepared photographic prints and drawings.

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Veliger Larvae of Carinariidae (Mollusca: Heteropoda) from Hawaiian Waters

by

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Abstract. Larvae belonging to four species of carinariid heteropods (*Pterosoma planum* Lesson, 1827, *Cardiapoda richardi* Vayssière, 1903, *Carinaria galea* Benson, 1835, and *Carinaria japonica* Okutani, 1957) were collected from near-surface waters (upper 100 m) around the Hawaiian islands of Molokai, Lanai, and Maui. Observations of live specimens were made aboard ship with dissection microscopes. Larval shell morphology was examined by SEM. The larvae of *P. planum* and *C. richardi* were identified by examination of individuals that underwent metamorphosis, while the identities of *C. galea* and *C. japonica* were determined subsequently by comparison with the protoconchs of juvenile and adult shells. The larvae of *P. planum*, *C. galea*, and *C. japonica* have not been described previously.

INTRODUCTION

Five species of carinariid heteropods have been reported from the plankton of Hawaiian waters. Four of these (*Pterosoma planum*, *Carinaria galea*, *Carinaria japonica*, and *Carinaria lamarcki*) were recorded by Seapy (1987), while the fifth, *Cardiapoda richardi* Vayssière, 1903, was collected more recently (February, 1991) from waters to the north of the island of Kauai (Seapy, unpublished data). Other records from the North Pacific are limited to California and Kuroshio Current waters. From the California Current off the west coast of North America, *C. japonica* has been reported by Dales (1953), McGowan (1967), and Seapy (1974, 1980). From Japanese waters, six species of *Carinaria* were recorded: *C. lamarcki*, *C. cristata*, *C. japonica*, *C. challengerii*, and *C. galea* by Okutani (1961), and *Pterosoma planum* by Okutani (1957).

Compared to the well-documented taxonomy of adult carinariids, the larval taxonomy is poorly known. The larvae of only three species have been described. Franc (1949), Richter (1968), and Thiriot-Quévèreux (1969, 1973) characterized the larva of *Carinaria lamarcki* from

the Mediterranean Sea. Subsequently, Thiriot-Quévèreux (1975) described the larvae of *Cardiapoda placenta* and *Cardiapoda richardi* from the North Atlantic Ocean and compared them with the larvae of *Carinaria lamarcki* from the same area. No descriptions of larval carinariids have been published from the Pacific or Indian Oceans. In the present study, identifications and descriptions of the larvae of four carinariid species from Hawaiian waters are given. Our observations of the larvae of *Cardiapoda richardi* support those of Thiriot-Quévèreux (1975) for this species from the North Atlantic Ocean. The descriptions of the larvae of *P. planum*, *C. galea*, and *C. japonica* are new. Thus the number of described carinariid larvae is increased from three to six. Based on the characterizations of these six larvae, we have attempted to identify larval characters that distinguish the three genera and the species of *Carinaria* and *Cardiapoda*.

MATERIALS AND METHODS

Specimens of carinariid larvae were collected during an 8-17 January 1992 cruise of the R/V *Moana Wave*, Uni-

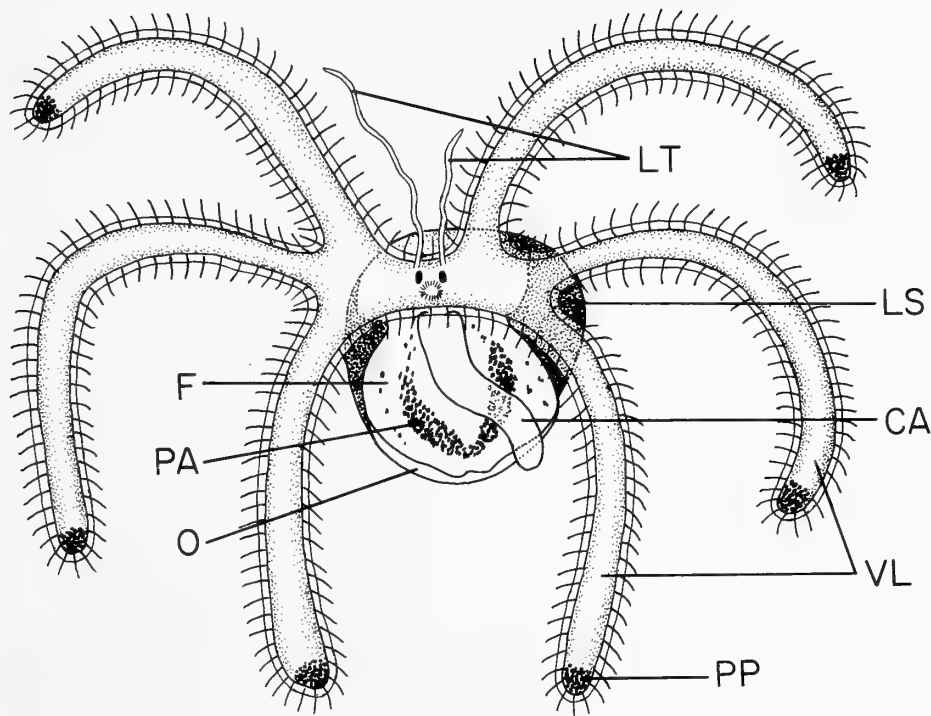


Figure 1

Generalized sketch of a carinariid larva (redrawn and modified from Thiriot-Quiévreux, 1975). Abbreviations: CA—cylindrical appendix; F—foot; LS—larval shell; LT—larval tentacles; O—operculum; PA—pigmented area of foot; PP—pigmented patch; VL—velar lobes, with ciliary bands represented schematically.

versity of Hawaii, to waters around the Hawaiian islands of Molokai, Lanai, and Maui. Oblique plankton tows to a target depth of 100 m were taken twice daily (early morning and late afternoon) throughout the cruise using a continuously open, 1-m plankton net (0.33 mm mesh). Plankton tows were sorted within 2 hr of collection, and larvae were transferred to finger bowls and petri dishes for observation under dissection microscopes. Specimens to be used later for examination of external shell morphology under the scanning electron microscope were preserved in 5% buffered seawater formaldehyde solution, and subsequently transferred to 70% ethanol solution. Specimens for on-board examination of soft part morphology and metamorphosis were kept in an air-conditioned laboratory at about 21°C in finger bowls and petri dishes, and the seawater was changed twice daily.

For SEM studies, shells of preserved specimens were cleaned by gently brushing away any debris present with very fine camel's hair brushes under a dissection microscope. They were mounted on aluminum stubs using double-sided tape, after which they were cold sputter-coated with gold-palladium (60:40), 21 nm thickness, in a Pelco Model 3 sputter coater. The shells were examined under a JEOL JSM-35CF scanning electron microscope, and photographs were taken on Kodak T-MAX 120 black-and-white negative film.

Since the larvae of two the species did not undergo metamorphosis during the cruise (see below), shells belonging to identified juvenile and adult carinariids were examined for comparison of their protoconchs with the larval shells. Representative shells from an adult *C. galea* from Hawaiian waters and a juvenile *C. japonica* from waters off Southern California were examined under SEM.

RESULTS

Four species of carinariid larvae were collected during the 10-day period of the Hawaiian cruise. Since the larvae could be distinguished easily on the basis of color and shell sculpture, we initially referred to them as species #1 (pink, smooth); #2 (tan-yellow, smooth); #3 (brown, spinose); and #4 (brown, smooth). Also, the number sequence conformed to their ranked order of abundance in the plankton samples. During the cruise, we examined a total of 59 specimens of species #1, 17 of species #2, 6 of species #3 and 5 of species #4.

Three specimens underwent metamorphosis at night during the cruise. Two individuals of species #1 metamorphosed on different nights and were immediately recognized as *Pterosoma planum* by the unique body shape of this species. As in other carinariids, the shell of *P. planum*

Table 1

Characteristics of late-stage carinariid larvae observed with dissection microscopes during a January 1992 cruise in waters around the Hawaiian islands of Molokai, Lanai, and Maui.

Species	Larval shell	Velum	Body coloration	Tentacles	Metamorphosis
<i>Pterosoma planum</i>	transparent	bordered by a thin line of pink pigment; dark red spot at end of each lobe	pink; purple digestive gland	colorless	time = one night; velum ingested; mid part of body oblong disk with pink patches
<i>Cardiapoda richardi</i>	transparent; umbilical striae conspicuous	bordered by a thin line of brown pigment; no terminal pigmentation	light yellow; light brown digestive gland	left tentacle colorless, right tentacle brown	time = one night; tail with dark brown membranous expansion
<i>Carinaria galea</i>	transparent; short spines in spiral rows	no bordering pigmentation; large dark brown patch at end of each lobe	brown; head light brown, stomach dark brown	colorless	not observed; identification by protoconch
<i>Carinaria japonica</i>	transparent; umbilical striae conspicuous	no bordering pigmentation; large dark brown patch at end of each lobe	brown	colorless	not observed; identification by protoconch

is situated dorsally on the body and covers most of the viscera, reproductive organs, heart, and gills. In carinariids, the body is drawn out in the anterior-posterior axis, and is approximately cylindrical. In *P. planum*, however, the central portion of the body is enlarged as a dorso-ventrally compressed oblong disk, and the proboscis extends ventrally beneath the disk. A single individual belonging to species #2 underwent metamorphosis. The presence of a dark-brown, cup-shaped, membranous expansion on the ventral surface of the tail identified this species as *Cardiapoda richardi*. This unique pigmented structure on the tail was seen also in newly metamorphosed *C. richardi* by Thiriôt-Quévèreux (1975). The larvae of species #3 and #4 did not undergo metamorphosis during the cruise, and their identity was based on comparisons of their shells with the protoconchs of adult and juvenile shells belonging to known species.

Larvae observed at late stages of development possess a series of features common to carinariid veliger larvae (Figure 1). These include: (1) a globular shell with an open

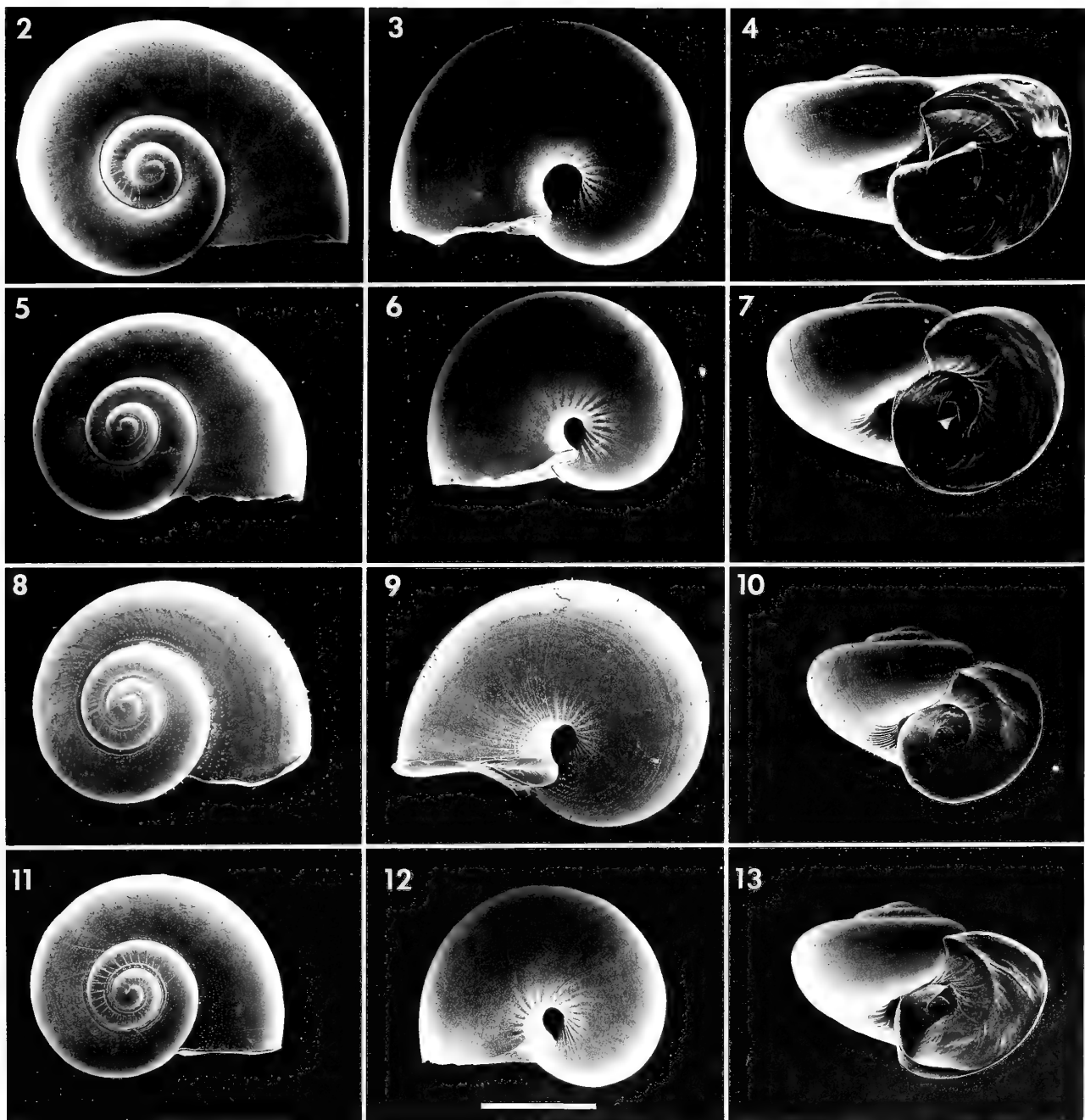
umbilicus marked with short, radiating striae; (2) a foot with a large opercular lobe and, arising anteriorly, a cylindrical appendix that extends like a mobile truck (also seen in pterotracheid larvae); (3) a velum consisting of six long and narrow ciliated lobes; and (4) well-developed tentacles of unequal size, the right being longer than the left. When the larvae were observed swimming, the right tentacle could extend to a length as great as the velar lobes. The tentacles and the cylindrical appendix are transitory larval organs that regress at metamorphosis (Thiriôt-Quévèreux, 1975). Following metamorphosis, the adult tentacles develop and are of unequal length, with the left longer than the right (Thiriôt-Quévèreux, 1975), and the cylindrical appendix becomes the sucker of the swimming fin (Franc, 1948, 1949).

Characteristics of the four larval types from Hawaiian waters essentially concern shell sculpture and pigmentation of the velum, tentacles, and body. These observations are summarized in Table 1. Detailed descriptions of the four larvae follow.

Table 2

Characteristics of late-stage carinariid larvae reported in Thiriôt-Quévèreux (1975).

Species	Larval shell	Velum	Body coloration	Tentacles
<i>Cardiapoda placenta</i>	transparent	bordered by brown pigment; two large brown patches on each lobe	light brown to none; yellow digestive gland	dark brown (right); light brown (left)
<i>Carinaria lamarcki</i>	transparent	bordered by thin line of brown pigment; small brown patch at end of each lobe	brown; yellow digestive gland	colorless



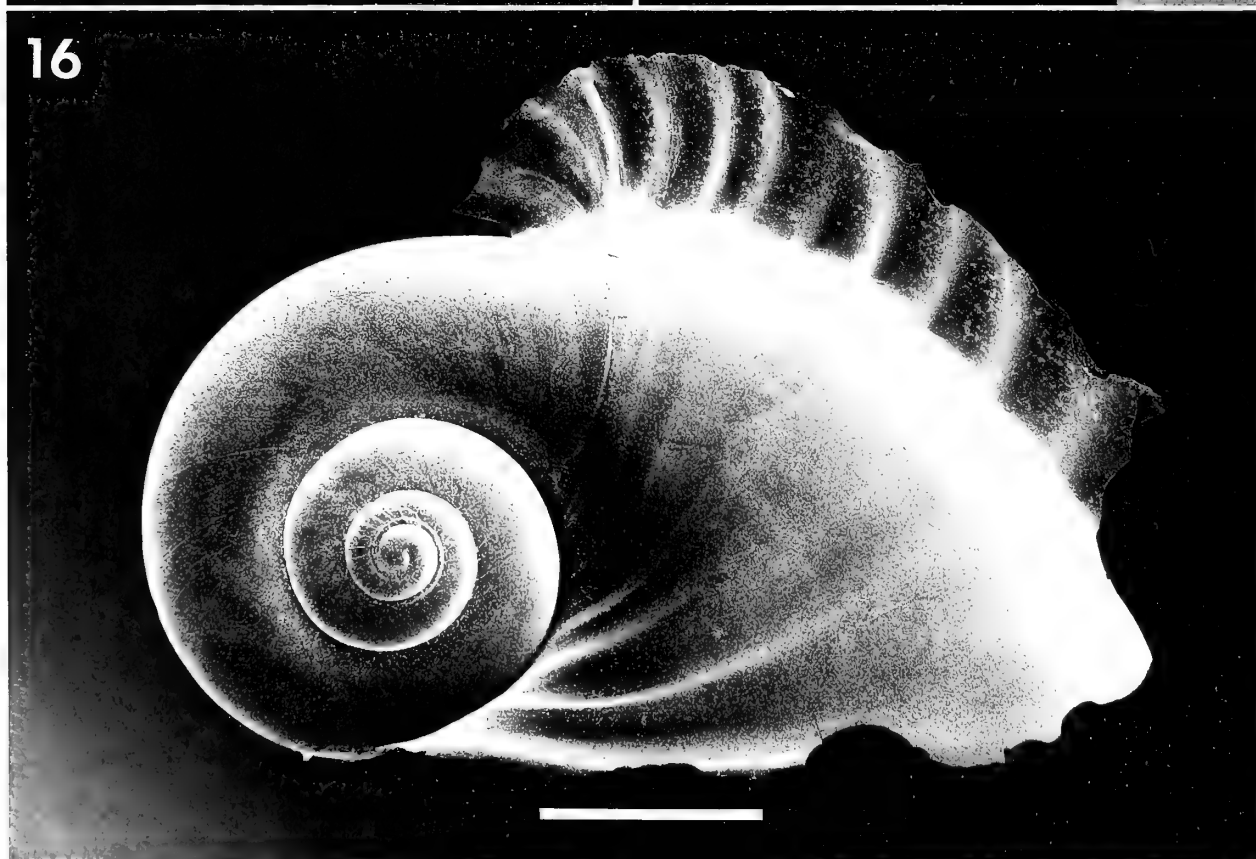
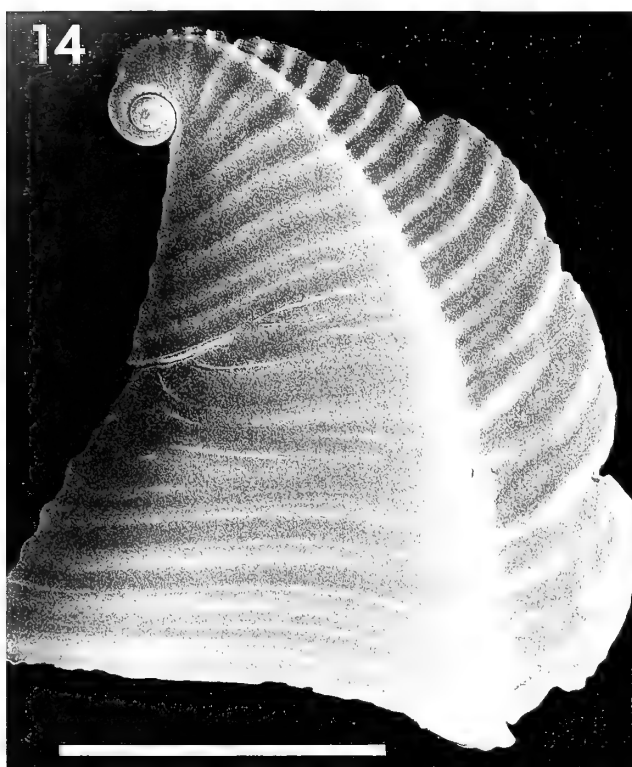
Explanation of Figures 2 to 13

SEM photographs of the larval shells from four species of Hawaiian Carinariidae, viewed from the right side, left side, and facing the shell aperture. All photographs at the same magnification; scale bar = 250 μ m. Figures 2-4, *Pterosoma planum*; Figures 5-7, *Cardiapoda richardi*; Figures 8-10, *Carinaria galea*; Figures 11-13, *Carinaria japonica*.

Pterosoma planum

The velum is bordered by a thin line of pink pigment. A dark red pigment spot is located on the terminal portion of each of the six velar lobes. The velar pigmentation is

less marked in older stages, and the red spot is often reduced, or even absent, in larvae close to metamorphosis. The body has an overall pink color, except for the tentacles, which are colorless, and the digestive gland which is purple. The shell is transparent. The right side of the shell



(Figure 2) is smooth except for narrow and low radiating ridges on the second shell whorl. The surface of the left side of the shell (Figure 3) is smooth except for about 13 low, radiating striae arising from the deep and wide umbilicus. The aperture is oblong (Figure 4), and the operculum has a spiral ridge with a narrow crest that is centered in the last opercular whorl.

Among the species of carinariids collected as adults from the epipelagic zone off Hawaii over the past 12 years (R. Seapy, unpublished data), *Pterosoma planum* is the most frequently captured. The dominance of this species in the Hawaiian carinariid fauna is correlated with its high proportionate representation among the carinariid larvae (59 of 87 specimens) collected during this study.

Cardiapoda richardi

A thin line of brown pigment borders the velum, and the velar lobes lack any terminal pigmentation. The body is light yellow, and the digestive gland is light brown. The left tentacle is colorless and the longer right tentacle is brown pigmented. Pigmentation of the velum and right tentacle is more pronounced in earlier than in later larval stages. The shell is transparent. The shell surface on the right side (Figure 5) is smooth, except for two elevated spiral ridges on the second whorl. This pair of elevated ridges is distinctive to this species, and is present in the same location on the shell of *C. richardi* from the North Atlantic (Thiriot-Quiévreux, 1975, fig. 1K, L). The umbilicus is deep but not wide (Figure 6), and is characterized by about 13 prominent and elevated radiating striae. The aperture is oblong (Figure 7), and the operculum has a broad and weakly defined spiral ridge centered in the last opercular whorl. Radiating, narrow striae extend from the medial margin of the last opercular whorl toward the spiral ridge. The larvae of *C. richardi* from Hawaiian waters are identical in pigmentation and morphology with those examined from the North Atlantic by Thiriot-Quiévreux (1975).

Carinaria galea

The velum lacks pigmentation except for a large, dark brown patch located at the end of each of the velar lobes. The body is brown, and the tentacles are colorless. The shell is distinguished by numerous, short spines (Figures 8, 9). These spines arise from low spiral ridges, which

become prominent on the last shell whorl. We observed this spinose ornamentation under the dissection microscope aboard ship. On the right side of the shell (Figure 8), an elevated spiral ridge is present adjacent to the inner suture, beginning on the second whorl. Outward and immediately adjacent to this ridge is a second spiral ridge that is narrow and low. The inner ridge ends at about whorl $3\frac{1}{4}$, while the outer ridge continues to the beginning of the fourth whorl. On the left side of the shell (Figure 9), the umbilicus is deep and intermediate in width between those of *Pterosoma planum* and *Cardiapoda richardi* (Figures 3 and 6, respectively). The radiating striae that arise from the opening of the umbilicus are narrow and low in contrast to the broader and more elevated striae seen on the other three species. The aperture is oblong (Figure 10), but is more elongate than in the other species. The operculum has a centered spiral ridge on the last opercular whorl that becomes progressively more elevated and peaked.

Since no larvae belonging to this species underwent metamorphosis, the identity of this larva was based on comparisons with protoconchs from adult shells. Examination of the protoconch on the adult shell of *Carinaria galea* (Figures 14, 15) reveals the distinctive short spines on the surface and the paired spiral ridges adjacent to the suture that characterize the larval shell (Figure 8).

Carinaria japonica

The velum is colorless except for the ends of each velar lobe, where a large, dark brown pigment patch is located. The body is an overall brown color. The head is light brown, the stomach dark brown, and the digestive gland an intermediate shade of brown. The tentacles are transparent. The shell is transparent, but has a brown appearance resulting from the coloration of the body. Very small and extremely numerous fine punctae are arranged in spiral rows on the shell surface (Figures 11, 12). This feature is not evident under the dissection microscope. On the right side of the shell (Figure 11), a distinctive pattern of sculpture is expressed on the second whorl. A prominent spiral ridge begins on the second whorl and ends at about whorl $3\frac{1}{4}$. A second, narrow outer spiral ridge appears briefly between whorl $2\frac{1}{2}$ and $2\frac{3}{4}$. A series of narrow, moderately elevated striae radiate outward from the spiral ridges on the second whorl. On the left side of the shell (Figure 12), the umbilicus is deep and comparable in width to that of *Carinaria galea*. About 18 broad and elevated

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Explanation of Figures 14 to 16

SEM photographs of the adult shell of *Carinaria galea* (Figures 14, 15) and a juvenile shell of *C. japonica* (Figure 16). Figure 14, shell viewed from right side; Figure 15, protoconch region of same shell from right side; Figure 16, juvenile shell viewed from right side. Scale bars = 5 mm (Figure 14) and 500 μ m (Figures 15, 16). Specimen of *C. galea* collected off Maui with an open, 1-m² plankton net towed obliquely to a maximal depth of about 150 m at 2100 hr on 13 February 1991. Specimen of *C. japonica* collected from San Pedro Basin, California with paired, 70-cm Bongo nets, towed between 70 and 110 m at 1515 hr on 30 March 1993.

striae radiate outward from the umbilical opening. The aperture (Figure 13) is oblong, and the operculum has a centered and crested spiral ridge on the last opercular whorl.

The identity of this larva was based on comparison with the protoconch of adult and juvenile *Carinaria japonica* (Figure 16). The prominent spiral ridge and radiating striae on the second shell whorl of the protoconch of *C. japonica* are distinguishing features of the larval shell.

DISCUSSION

The three genera that compose the family Carinariidae are represented among the four species characterized in this paper. Taxonomic differences that distinguish the genera are well documented for adults. However, since the larvae of only three species have been described previously (Thiriôt-Quévèreux, 1975), larval taxonomic features at the generic level have not been examined. As adults, all three genera possess an elongate, gelatinous, and largely transparent body. The opaque internal organs, including the stomach, digestive gland, intestine, kidney, gonad, and heart, are contained in a stalked, mid- to postero-dorsal visceral mass (Lalli & Gilmer, 1989). The visceral mass is covered by a transparent shell in *Carinaria* and *Pterosoma*, while the shell is reduced and embedded in apical tissues of the visceral mass in *Cardiapoda*. The external adult shells of *Carinaria* and *Pterosoma* are markedly different. In *Carinaria*, the shell is tall and triangular in shape, enclosing the visceral mass, while in *Pterosoma* the shell is dorso-ventrally flattened, forming a broad cap over the compressed visceral mass (Seapy, 1987).

Descriptions of larval carinariids in this study (Table 1) and previously by Thiriôt-Quévèreux (1975; summarized here in Table 2) enable us to propose generic-level differences among the larvae. Comparisons of larval shell morphologies within the genera *Carinaria* and *Cardiapoda* show no consistent characters, although these differences can be used to distinguish the species within each genus (discussed below). The only characters that appear to be useful at the generic level are based on pigmentation. The larvae of both species of *Cardiapoda* have brown right tentacles, whereas the tentacles in the other two genera are colorless. The coloration of *Pterosoma* larvae is pink; the larvae of other genera are brown or yellow. Body coloration in the three species of *Carinaria* examined to date is brown, whereas *Cardiapoda* is lightly colored (yellow or brown) or colorless. Descriptions of larvae belonging to the remaining species of *Carinaria* are required to determine whether or not the brown body coloration can serve as a generic characteristic.

Within the genera *Cardiapoda* and *Carinaria*, larval shell ornamentation is variable. These differences, along with pigmentation characteristics, can be used to distinguish the larvae. In *Cardiapoda*, two elevated spiral ridges are present on the second shell whorl (Thiriôt-Quévèreux, 1975). In *C. placenta*, these ridges are weakly developed, and the

outer ridge only extends for about one-third of the second whorl. In *C. richardi*, both ridges are well developed. The velums of the two species also differ (Tables 1 and 2); there are two large brown patches on each lobe in *C. placenta*, whereas there is no terminal lobe pigmentation in *C. richardi*. Among the three species of *Carinaria*, *C. galea* has numerous short spines that arise from low spiral ridges, *C. japonica* has a prominent spiral ridge from which striae radiate outward on the second shell whorl, and *C. lamarcki* has a pair of prominent spiral ridges on the second whorl (Thiriôt-Quévèreux, 1975). Since the shells of the latter two species are similar in appearance, the larvae can be distinguished on the basis on velar pigmentation (Tables 1 and 2). The velar lobes are bordered by a thin line of brown pigmentation and have a small, terminal, dark brown patch in *C. lamarcki*, whereas there is a large dark brown patch at the end of each velar lobe and bordering pigmentation is lacking in *C. japonica*.

ACKNOWLEDGMENTS

We thank Richard Young of the Department of Oceanography, University of Hawaii for inviting us to participate in his January 1992 cruise aboard the R/V *Moana Wave*. We are grateful to him for providing us with the plankton net, sufficient daily sampling time, laboratory space, and dissection microscopes. We thank Captain Jim Cvitanovich and the crew of the R/V *Yellowfin* for their assistance during the Bongo Net cruise of March 1993. We are most appreciative of Steven Karl, California State University, Fullerton, for operation of the SEM, photography, and printing of the photographic plates in the paper. This is Contribution No. 73, Ocean Studies Institute, California State University.

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The Fine Morphology of the Shell Sac in the Squid Genus *Loligo* (Mollusca: Cephalopoda): Features of a Modified Conchiferan Program

by

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Abstract. The supposedly ancestral chambered shell design is conserved in only a few extant cephalopod groups (in the ectocochlean Nautiloidea and in two families of the endocochlean Coleoidea: Sepiidae, Spirulidae); the majority of living cephalopods have purely organic shells or shell relics produced by secretory epithelia of the closed shell sac which lies in the dorsal part of the muscular mantle. The ultrastructure of these epithelia is described here from a loliginid squid, providing the basis for discussing the extent of phyletic conservation of the "conchiferan program" in a highly modified morphogenesis. The squid shell development omits both chamber formation (the ancestral cephalopod program related to a calcified shell) and shell calcification (the ancestral conchiferan program), but shows features that are recognizable as conserved elements of the conchiferan mode of shell formation. The greatly "simplified" squid shell development is interpreted as part of an adaptive process by which full integration of the shell into a highly flexible muscular mantle was achieved.

INTRODUCTION

About 700 living cephalopod species are known to science; one percent of these (genus *Nautilus*) represent the subclass Nautiloidea Agassiz, 1847; the others are members of the subclass Coleoidea Bather, 1888 (see Nesis, 1987 for an overview). In contrast to *Nautilus*, which is the only living representative of the original cephalopod design characterized by a calcified *outer* shell with chambers and a siphuncular tube (Denton & Gilpin-Brown, 1973; Yochelson et al., 1973), the "modern" Coleoidea have their shell enclosed in a shell sac, the upper (or outer) part of which is derived from the embryonic mantle integument. This sac is sealed during early organogenetic stages; it undergoes various modifications through later embryonic stages that foreshadow the more or less "rudimentary" morphology of the adult shell to be developed (if not entirely suppressed). The general trends of ontogenetic modification of the shell sac in coleoid cephalopods are well known for the decapodan orders Sepioidea Naef, 1916 and Teuthoidea Naef, 1916 (the latter comprising the inshore Myopsida, including *Loligo*, and the offshore Oegopsida), the

monotypic order Vampyromorpha Pickford, 1939, and the order Octopoda Leach, 1818 (see Boletzky, 1982 for a review). However, relationships among these higher taxa of living cephalopods and their respective ancestors, which have left a long and diverse but naturally incomplete fossil record, are still debated (Clarke & Trueman, 1988; Teichert, 1988; Boletzky, 1992).

The difficulties in relating extant and extinct forms arise in part because the majority of modern coleoid cephalopods possess an uncalcified shell or "gladius" providing relatively limited information on characters that are conserved in the fossil forms (Donovan & Toll, 1988). Similar problems arise even with more resistant hard structures that may be preserved in the fossil record, e.g., beaks (Clarke, 1986), statoliths (Clarke & Maddock, 1988), and hooks (Engeser & Clarke, 1988).

The limited information retrievable from gladius structures nonetheless offers new insights. Systematic studies dealing with the morphometrics of the gladius of extant teuthoid squids and work analyzing the information for age determination are drawing increasing attention in applied research, especially in the field of fisheries biology

(Toll, 1982, 1988, 1990; Donovan & Toll, 1988; Alexeyev, 1989; Bizikov, 1987, 1991). But along with refinement of techniques for applied studies, there is also the need to elucidate the basic biological mechanisms underlying the formation of the periodic chitin-proteoglycan structure of the squid gladius, which is characterized by laminated "plywood" material somewhat similar to arthropod cuticle (Hunt & El Sherief, 1990; see Tevesz et al., 1992 for complementary information on shell matrix composition in *Nautilus*).

The morphogenesis of the shell sac, with its glandular cells that secrete the shell material, has been studied in different coleoid species with the light microscope (Appellöf, 1893, 1898; Boletzky, 1964; Spiess, 1972). In contrast, no electron microscopical study describing the ultrastructure of a shell sac that produces an uncalcified gladius is available. The ultrastructure of the adult shell sac epithelia has so far been described only in *Sepia*, where the architectural conditions are complicated by the chambered shell design (Wendling, 1987). The general processes of growth in cuttlebones (Tanabe et al., 1985) and in the *Nautilus* shell are relatively well understood (Ward & Chamberlain, 1983; Arnold et al., 1987), but a new theory of shell calcification based on the observation of *Nautilus* embryos (Arnold, 1992) now requires a very careful reassessment of earlier data on the ultrastructure of the cells that are involved in the formation of calcified cephalopod shells (See Bandel, 1990 for a review). This problem will have to be dealt with in future studies; it is not discussed in the present context.

In this paper, we describe the ultrastructural morphology of the shell sac in the myopsid squid *Loligo vulgaris*, with complementary information obtained in *Loligo opalescens*, based on transmission electron microscopy. Our discussion deals with the question of whether the *Loligo* shell sac can be compared directly with the shell-forming tissues of other conchiferan mollusks, focusing mainly on the outer and middle mantle folds in bivalves and gastropods. Within those two classes, the mantle folds secrete the periostracum and shell; therefore they appear homologous to the shell gland in the Cephalopoda (Moor, 1983).

By leaving aside the question of *how* (in terms of cell differentiation) the original cephalopod mode of calcification and chamber formation could have been "removed" from the morphogenetic program of an ancestral teuthoid squid, we are able to hypothesize about *why* it disappeared. The retrospective "top-down view" of phylogenetic reconstruction merely allows us to assume that the ability to produce a calcified shell was "lost" somewhere along the teuthoid line, but it does not provide a functional explanation for this loss. To approach this *why* question, we have to turn to the basically prospective "bottoms-up view" of evolutionary (constructional) morphology, which focuses attention on the adaptive *advantages* related to the obvious "loss" of chamber formation and shell calcification. This will be the final point in our Discussion.

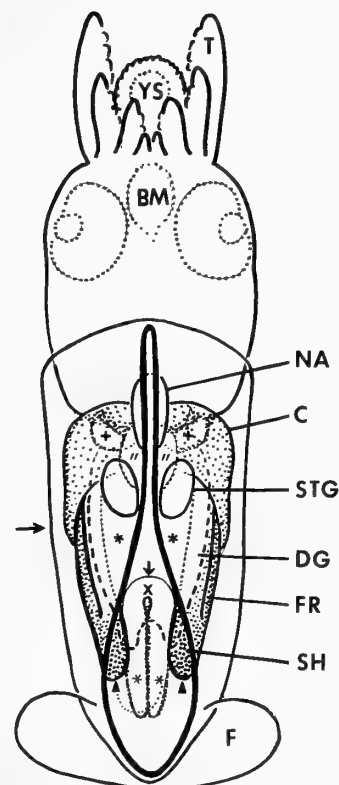
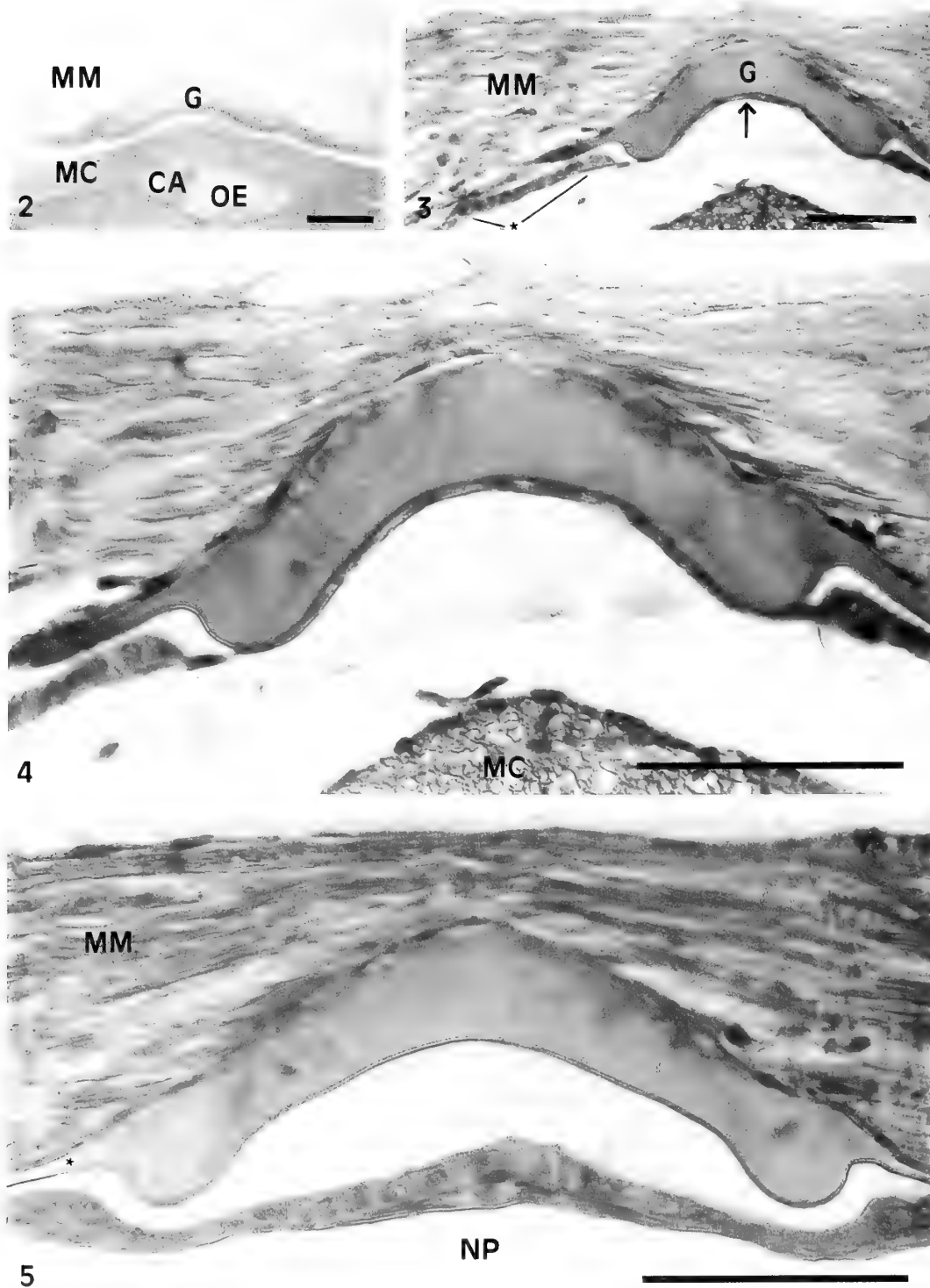


Figure 1

Loligo vulgaris hatchling measuring 2.8 mm in dorsal mantle length, semischematic representation in dorsal view (reconstruction from histological cross sections; note that the mantle is contracted due to tissue shrinkage during fixation). The shell sac (SH) enclosing the gladius is drawn out anteriorly, beyond the stellate ganglia (STG), into a narrow part containing the rachis; the broad posterior half houses the vane, which reaches under the bases of the fins (F). Due to the tissue contraction, the head is partly withdrawn into the mantle so that the anterior end of the rachis reaches beyond the nuchal attachment (NA) on the dorsal side of the collar (C); only the posterior surfaces of the statocysts (+) are visible, partly through the posterior salivary gland (*). The paired diverticula of the digestive gland (DG) lie on either side of the inner yolk sac (*); the latter reaches posteriorly (past the dorsoventral passage x of foregut and cephalic aorta) and forms two diverticula (*); the outer yolk sac (YS), which lies in front of the buccal mass (BM), is nearly empty and much shorter than the tentacles (T). Arrow heads point at the insertions of the funnel retractors (FR) on the ventral side of the vane wings; the small arrow close to x points at the posterior edge of the muscular capsule of the visceral mass (MC in following figures). The large arrow to the left indicates the area represented by Figures 2-4 and 6.

MATERIALS AND METHODS

Hatchlings of the European squid *Loligo vulgaris* used in this study were obtained from eggs collected at depths of 20-40 m with a benthic trawl by the Laboratoire Arago research vessel *Nereis*. The eggs were held in aquaria



supplied with fresh seawater at a rate of 150–200 L/hour at ambient temperature (12° to 15°C) and under ambient light conditions during the months of March and April. One- to two-day-old hatchling squid were collected from the aquaria and fixed immediately, after the protocol of Gilly, Hopkins, and Mackie (Gilly et al., 1991).

A three-step fixation was employed followed by enbloc staining with uranyl acetate. Hatchlings were fixed either whole or with the ventral mantle cut longitudinally from the anterior margin along its full length. Cutting the mantle was carried out to aid the penetration of fixative to the ventral layer of the shell gland.

The primary fixative consisted of a 1.5% glutaraldehyde solution with 10 mM CoCl₂, 10 mM MgCl₂, and 25 mM sodium cacodylate at a pH of 7.4. The osmolality was adjusted to 0.980 osmol with sucrose. Hatchlings were immersed for five minutes in the fixative to reduce the calcium ion concentration in the tissues, and then fixed for 1 to 4 hours at room temperature, cooling during the final half hour to 4°C.

The hatchlings were then postfixed on ice with an 8% K₃Fe(CN)₆, 0.5% OsO₄ solution buffered with 200 mM sodium cacodylate at a pH of 7.3 (before addition of the osmium) and adjusted to 1.200 osmol with sucrose. Fixations of 30 to 120 minutes duration were employed.

The final fixation was with 0.15% tannic acid in a 0.760 osmol sucrose solution buffered with 25 mM sodium cacodylate at pH 7.3. This fixation was carried out for 2 to 3 minutes with agitation at room temperature in a dark chamber.

Enbloc staining with 4% aqueous uranyl acetate solution was then applied for a minimum of 3 hours at room temperature with agitation on a shaker table of 100 RPM.

Washing of the tissues between fixation steps was done with a cold 25 mM sodium cacodylate buffered sucrose solution at a pH of 7.4 and tonicity of 0.980 osmol for 15 minutes.

Fixed material was dehydrated in graded hexalene glycol (2-methyl-2,4-pentadiol) and embedded in Spurr's resin. Hatchlings were sectioned on an LKB 8800 Ultratome III microtome to obtain both transverse sections at points along the longitudinal axis of the gladius and sagittal sections through the gladius (Figure 1). Sections were examined, without further staining or after staining for 2 to 5 minutes with Renoyld's lead citrate, on a Hitachi H-600 transmission electron microscope at 75 kV.

Micrographs of advanced juvenile and subadult opalescent inshore squid *Loligo opalescens* were done at Stanford University's Hopkins Marine Station. Individuals of 5 to 6 cm mantle length were collected with a hand net in Monterey Bay and maintained in a tank supplied with continuous flowing seawater at ambient temperature. Transverse sections 5 × 0.5 mm of dorsal mantle including the gladius were excised from living squid with a razor blade. The material was fixed with a protocol similar to that described above with the exception that the final fixation with tannic acid and the enbloc staining with uranyl acetate were both omitted. Transverse sections and sections oblique to the dorsal ventral plane of the animal were cut on a Porter Blum MT-2B microtome. Sections both with and without lead citrate and uranyl acetate staining were examined on a Phillips 301 transmission electron microscope at 60 kV.

For topographical orientation, a *Loligo vulgaris* hatchling was reconstructed from serial cross sections (Figure 1), and two cross sections of the shell sac in a laboratory-

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Explanation of Figures 2 to 5

Figure 2. Cross section of the dorsal part of the mantle and visceral mass in a *Loligo vulgaris* hatchling (semi-thin section of resin-embedded specimen). Scale bar 50 μm. The gladius (G) is narrow in the intermediary zone between the free rachis and the vane; the dorsal mantle muscle (MM) nearly closes over the dorsal shell sac epithelium; the muscular capsule (MC) of the visceral mass completely covers the esophagus (OE) and cephalic aorta (CA).

Figure 3. Cross section (paraffin-embedded material) of the shell sac in a one-month-old *Loligo vulgaris* measuring 5.2 mm in dorsal mantle length; section from a position similar to Figure 2. Scale bar 50 μm. Note the thin medial part of the ventral epithelium underlying the thick rachis of the gladius (G), and the much thicker marginal epithelium (*) underlying the wings of the vane. This is the situation typical of the anterior part of the vane, whereas in the posterior part (behind the insertion of the funnel retractors, see Figure 1), the ventral shell sac epithelium is thin even below the wing margins. Same abbreviations as in Figure 2.

Figure 4. Same as Figure 3, at higher magnification. Scale bar 50 μm. Note the nearly tangential insertion of the mantle muscle on the extremely thin dorsal shell sac epithelium. The large open space between the ventral shell epithelium and the muscular capsule of the visceral mass (MC) is artefactual.

Figure 5. Cross section of the rachis from the same specimen as Figures 3 and 4, but in a more anterior position, between the stellate ganglia (cf. Figure 1). Scale bar 50 μm. The muscular sheet (MM) covering the dorsal shell sac epithelium is somewhat thicker than in Figure 4, whereas the rachis is thinner and broader and shows lateral "ribs" more distinctly; the anterior continuation of the lateral wings is very narrow (*). The medial part of the ventral shell sac epithelium (artefactual separation from shell surface) is nearly as thick as the marginal parts, as is typical for the entire length of the free rachis. Note that the ventral shell sac epithelium is covered ventrally by a thin epidermis above the nuchal pouch (NP).

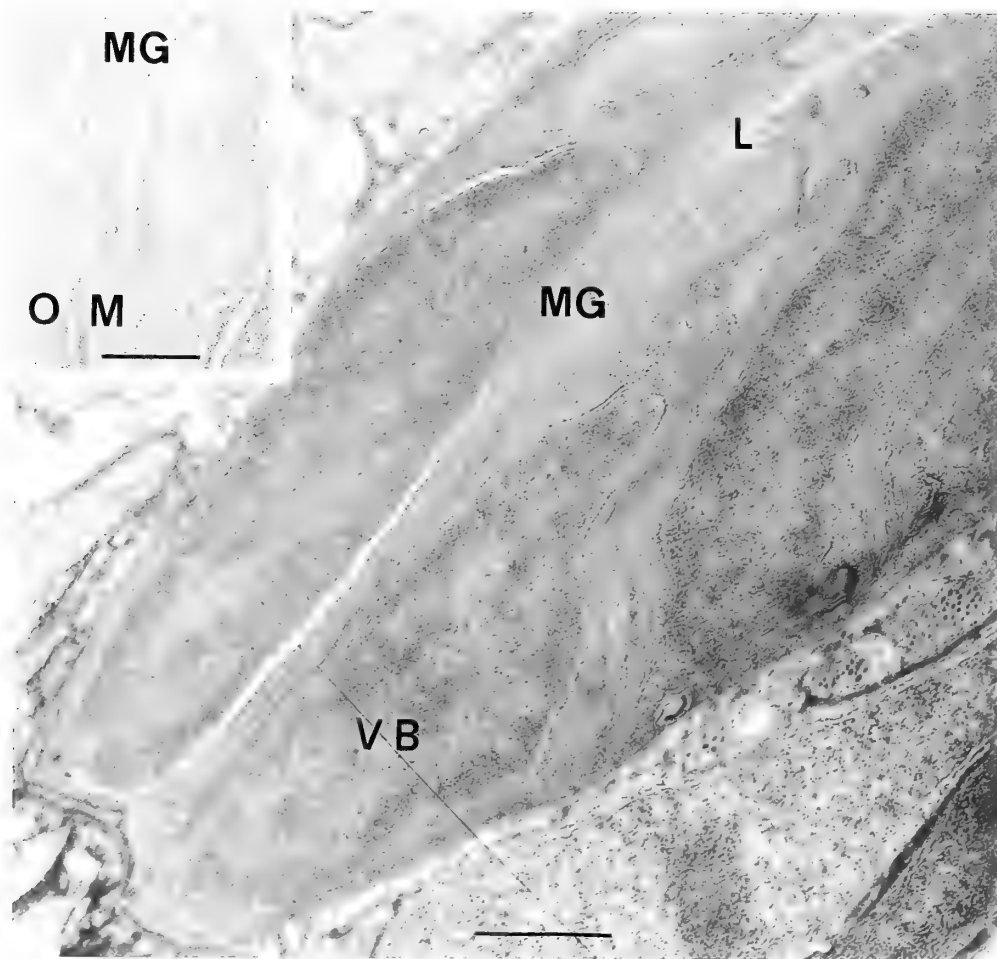


Figure 6

Cross section of shell sac in *Loligo vulgaris* hatchling, showing the basal cells at the margin of the shell sac toward the anterior end of the vane, dorsal side above, ventral side below (DB—dorsal basal cell; VB—ventral basal cell; MG—marginal gutter, L—lumen of shell sac). Scale bar 1 μm . Inset: detail of the opposed membranes (OM) and marginal gutter between basal cells. Note long microvilli. Scale bar 0.2 μm .

reared juvenile *Loligo vulgaris* are shown for comparison of tissue thickness in the primary epithelium underlying the anterior vane and rachis (Figures 3–5).

Gross morphology: The shell sac in *Loligo* consists of an invaginated monolayer of ectodermal cells composed of two distinct zones—one “ventral,” adjacent to different parts of the dorsal surface of the visceral mass (Figure 2) and to the nuchal attachment in the anterior extremity; the other “dorsal,” underlying the dorsal surface of the mantle (Figures 3–5). These two zones of shell-forming epithelium are also called the primary and secondary zones, respectively, because the ventral zone is derived from the primary shell field, which is delimited by the primordium of the mantle muscle at early organogenetic stages (Naef, 1928). The dorsal zone is then called secondary, because it is subsequently formed by the “ceiling” of the cavity

under the secondary cover, which is derived from a circular fold closing over the primary zone. The embryonic shell sac of coleoid cephalopods always starts out with a roughly circular outline, but soon becomes elongate in the body axis in all the decapods (transverse elongation in the octopods).

In the *Loligo* hatchling, the shell sac and gladius are characterized by a broad, rounded posterior half representing the vane, which is almost semicircular in cross section; anteriorly it tapers into the narrow rachis (Figure 1), which is the continuation of the middle rib; it is bow-shaped in cross section and markedly thicker than the vane (Figures 3–5). The dorsal side of the shell sac is largely covered by the muscular tissues of the mantle and, at its posterior end, of the fin bases. The latter will be “decoupled” from the shell sac during early juvenile development, with formation of so-called articular pouches (Boletzky,

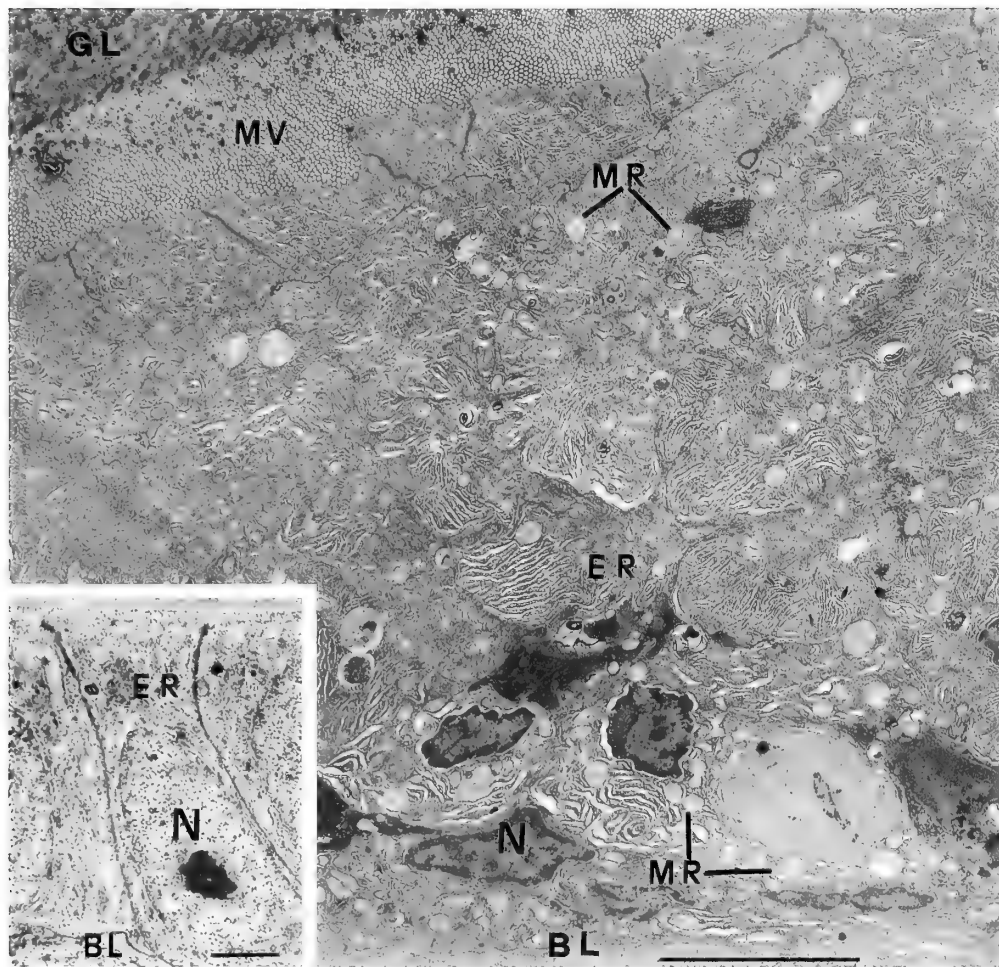


Figure 7

Oblique section of ventral shell sac epithelium in advanced juvenile *Loligo opalescens*, showing the columnar epithelium (cf. inset) close to the shell sac margin at the base of the free rachis. Note the broad band of obliquely cut microvilli (MV) underlying the gladius (GL), the abundant rough endoplasmic reticulum with dilate cisternae (ER), and mitochondria (MR) close to the microvillous border and to the nucleus (N) (BL—basal lamella). Scale bar 5 μm . Inset: same area in cross section. Scale bar 1 μm .

1982). The ventral side of the shell sac is in contact with different muscular tissues except in its anterior and posterior extremities. From the broadest part of the vane anteriorly, the joint muscular bases of the funnel retractors and visceral capsule form a pair of lateral insertions. Slightly anterior to the separation of the retractors from the muscular capsule (Figure 1), the latter closes over the dorsal surface of the visceral mass (containing the remaining inner yolk sac at the moment of hatching). More anteriorly, close to the stellate ganglia, the contact between the shell sac and the muscular capsule of the visceral mass is interrupted by the nuchal pouch. Here the shell sac lies close to the inner surface of the mantle where it forms the counterpart of the nuchal attachment covering the dorsal collar junction (Figure 1).

Ultrastructure: All the luminal surfaces of the shell sac epithelia are microvillous; there are short microvilli on the dorsal layer and tall microvilli on the ventral layer notably close to the margin. The entire shell sac is ensheathed by a basal lamella. In hatchling squid, muscle tissue is found adjacent to the basal lamella. In adults, connective tissue is present between the basal lamella and the surrounding mantle muscle tissue.

Five morphologically distinct cell types are present in the shell sac of *Loligo*: basal cells at the margin, low cells of two distinct morphologies in the dorsal layer, and tall cells of two distinct morphologies in the ventral layer (Figures 3–5, cf. Figure 16B).

The dorsal and ventral layers of basal cells join together at the margin of the sac; typically the dorsal layer is more

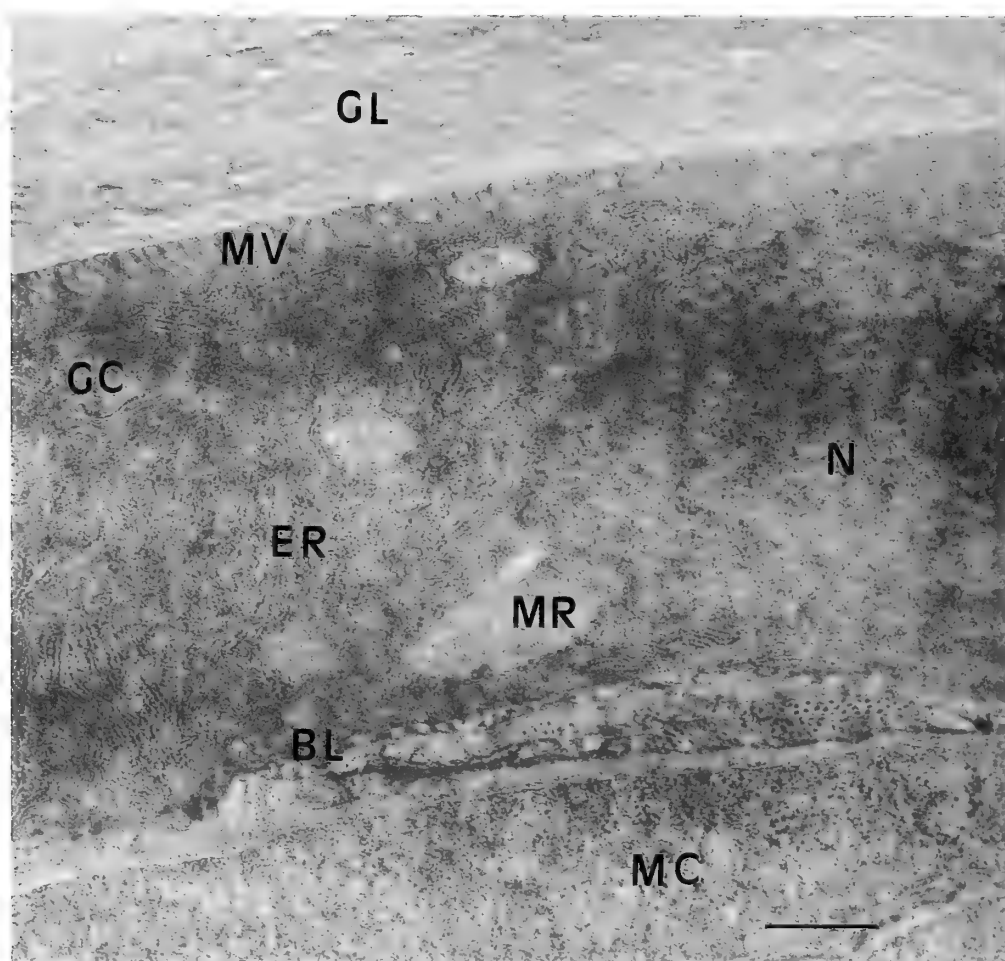


Figure 8

Figure 8. Cross section of shell sac in *Loligo vulgaris* hatchling, showing the cuboidal cells of the ventral epithelium close to the longitudinal axis of the rachis (cf. Figure 5). The gladius (GL), which shows its laminated structure, is in contact with relatively short microvilli (MV). Note the large nucleus (N), the extensive rough endoplasmic reticulum (ER), the apical position of the golgi complex (GC) and the mitochondria (MR) in various positions; the shell sac epithelium is separated from the underlying muscle cells (MC) by the basal lamella (BL). Scale bar 1 μm .

compressed. Both layers of cells possess large nuclei and prominent golgi complexes. The microvillous surfaces of the distal ends of the basal cells limit the margin of the lumen of the shell sac, which is slightly expanded, forming a marginal gutter. The microvilli of the dorsal cells are short compared to those of the ventral cells, except in the area of the marginal gutter where both cells extend long microvilli (Figure 6).

The cells close to the margin in the ventral layer of the shell sac are columnar in appearance. They possess large basal nuclei, abundant rough endoplasmic reticulum with dilate cisternae, long microvilli, and apical golgi complexes; mitochondria are found in association with the nucleus and with microvillous membranes (Figure 7).

Toward the longitudinal axis of the gladius, the ventral

cells are cuboidal in appearance. They possess large nuclei with the other components as described for the ventral marginal cells present, but relatively reduced; this appears to be in relation to the reduced cytoplasmic volume. The microvilli are also reduced in height compared to those at the ventral margin (Figure 8).

The cells in the dorsal portion of the shell sac form a thin layer of uniform height. Toward the margin, they stain darkly, exhibit short microvilli, and are rich in poly-somes, mitochondria and golgi complexes (Figure 9).

Over the longitudinal axis of the gladius, the cells typically stain more lightly (Figure 10). Bands of fibers run from the region close to the basal lamella to that of the gladius where they separate into smaller bands which fan out toward the microvillous membrane. Examination of

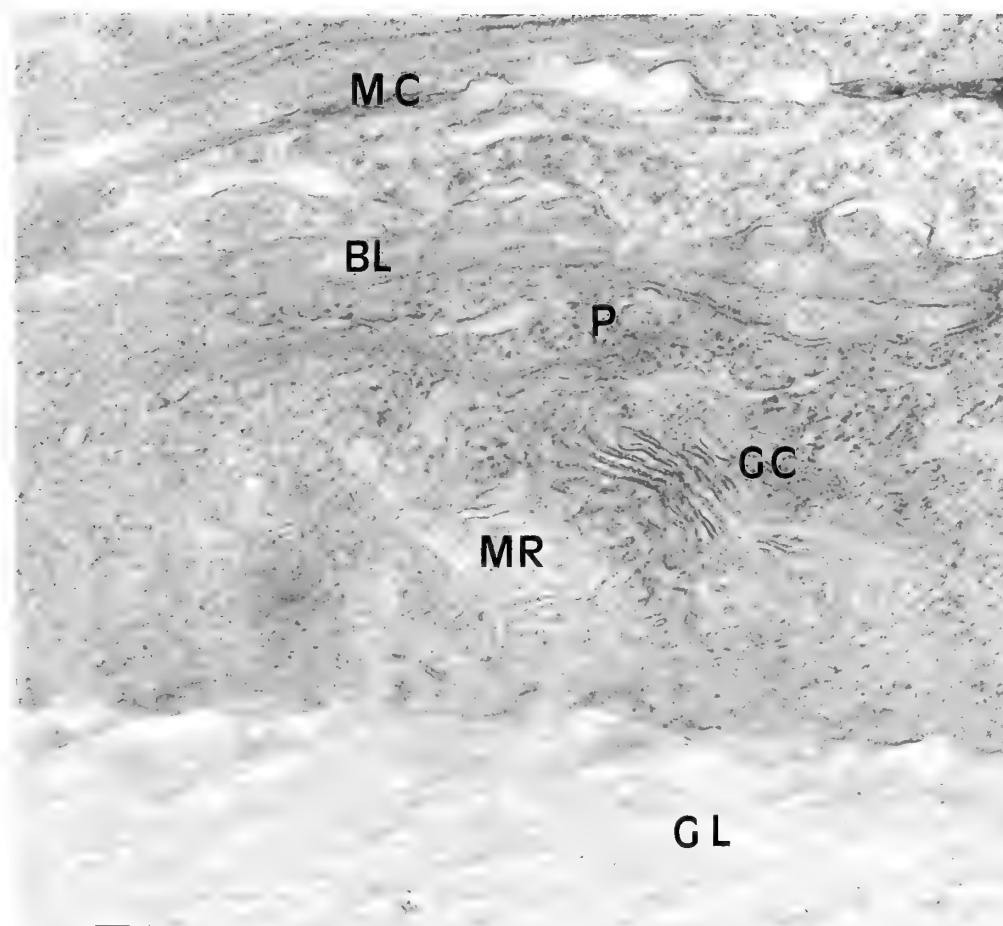


Figure 9

Cross section of anterior part of the shell sac in hatchling *Loligo vulgaris*, showing one of the flat cells of the dorsal epithelium, with nearly smooth cell surface in contact with the gladius (GL). Note mitochondrion (MR), a golgi complex (GC), and polysome (P), the latter lying close to the basal lamella (BL), which is covered dorsally by muscle cells (MC). Scale bar 0.5 μ m.

the fibers at high magnification shows them to consist of flat bands of microtubules evident from their oval cross sections (Figure 13); bundles of microfilaments are also present (Figure 14). These cells exhibit a complex interdigitation with the basal lamella (Figure 11); opposite the regions of interdigitation, myofibrils of the adjacent muscle cells can be observed (Figure 12).

DISCUSSION AND CONCLUSION

The squid gladius studied in this paper is homologous to the cuttlebone of sepia, as demonstrated by the identical positional relationships with the muscular mantle and fins, and by the identical overall morphogenesis of the shell sac (Appellöf, 1893; Naef, 1928; Boletzky, 1964; Spiess, 1972). As indicated in the Introduction, we cannot yet answer

convincingly the question of whether the uncalcified gladius is homologous to the entire organic matrix of the cuttlebone or only to the organic components of the unchambered dorsal shield. This question will have to be addressed again because we know of two shell variants that lie somewhere between the patterns observed in the sepiid cuttlebone and the loliginid gladius. On the one hand, there are fossil remains of gladiuslike "teuthid" shells (e.g., *Plesiotheuthis*) that were probably calcified without showing the chambered "phragmocone" part (Donovan & Toll, 1988); on the other hand, certain extant oegopsid squids (e.g., *Gonatus*, *Promachoteuthis*, and *Histioteuthis*) have a gladius without traces of calcification, but with a stratified gelatinous mass suggesting the presence of an uncalcified representative of the cuttlebone "chambers" (Toll, 1982, 1988).

Although the question of epithelial cell homologies in cuttlefish and squid shell sacs requires further study, our

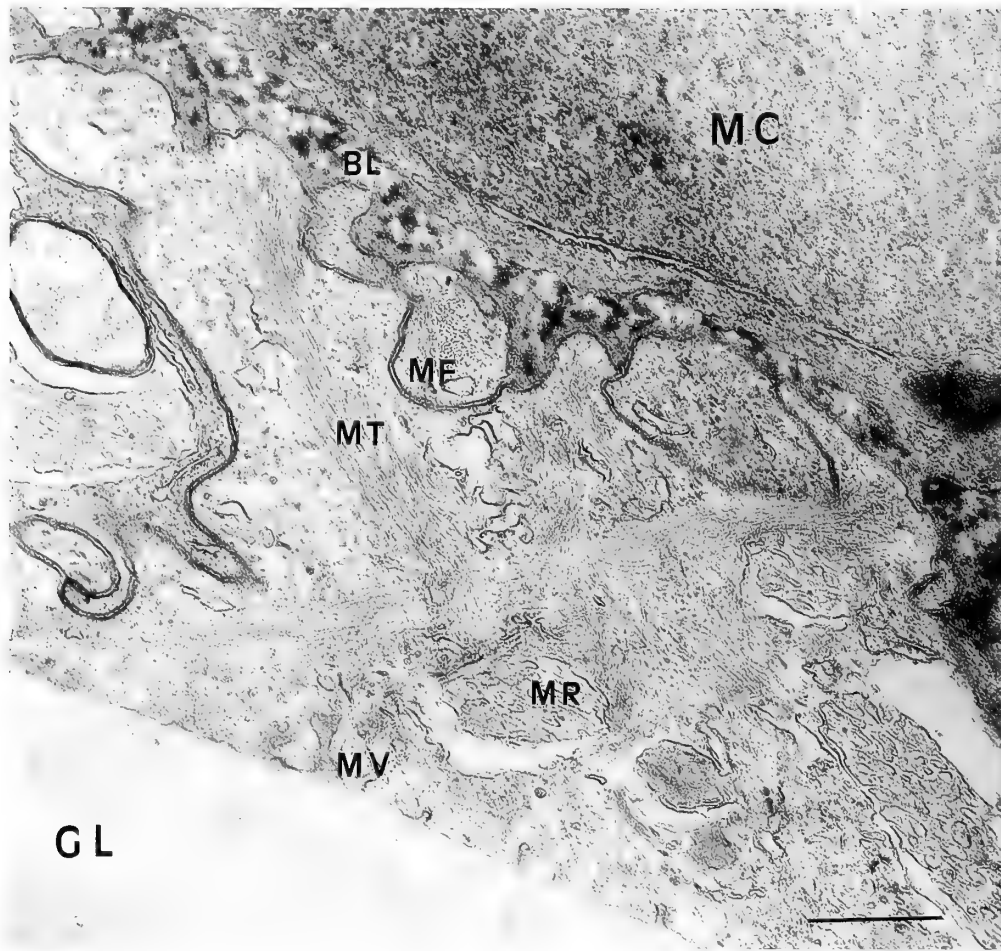


Figure 10

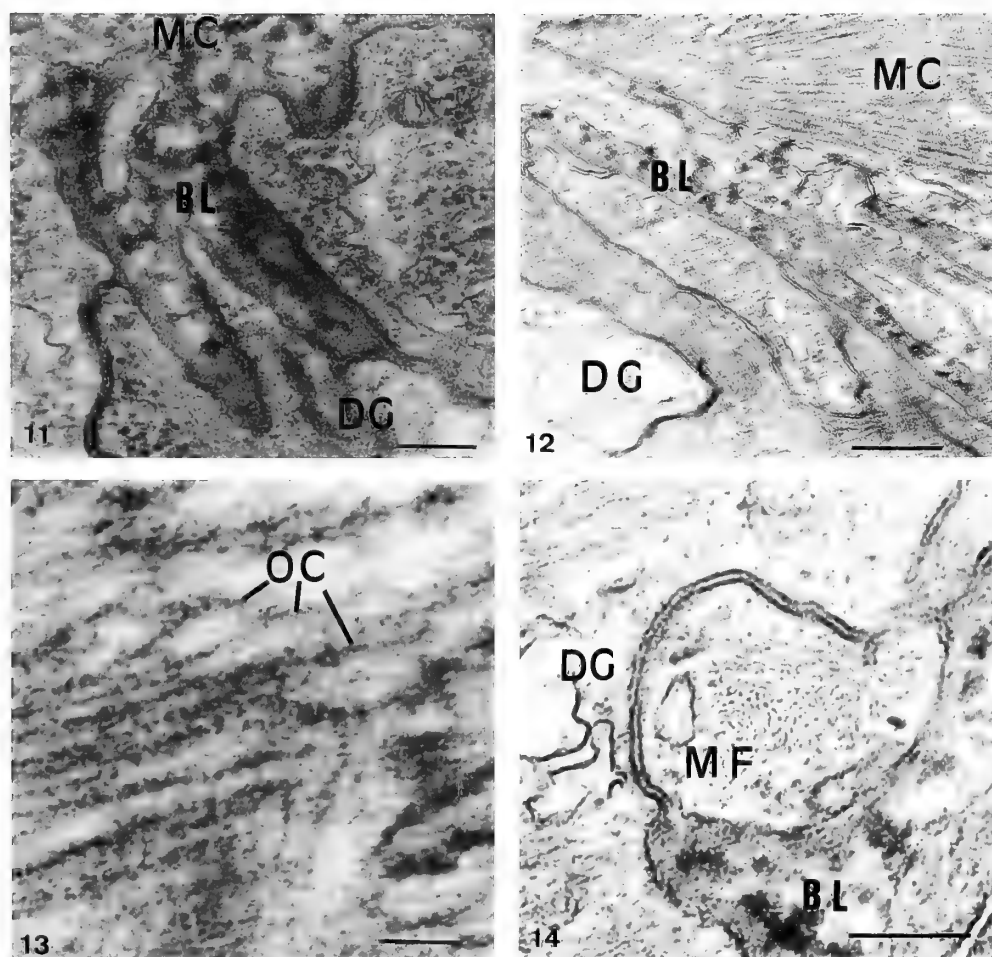
Cross section of dorsal shell sac epithelium close to the longitudinal axis in hatchling *Loligo vulgaris*. The interdigitated cells have only short, broad microvilli (MV) in contact with the gladius (GL). Note the strands of microtubules (MT) and microfilaments (MF) crossing the cells in different directions (other abbreviations as in preceding figures). Scale bar 0.5 μ m.

observations on the ventral (i.e., the primary) epithelium already suggest that in *Loligo*, there are no traces of a siphuncular epithelium, and apparently also no portion specialized for the formation of "septal" material in the ventral concavity of the gladius. Thus the supposed absence of the entire phragmocone complex makes the loliginid gladius appear sufficiently "simple" to permit some comparisons with the organic components of typical molluscan shells. e.g., those of bivalves or gastropods.

Early morphogenetic processes: Shell formation in gastropod and bivalve mollusks begins with the development of the shell field (cf. Bandel, 1982). The shell field first appears as a transitory invagination in the central area of the dorsal mantle epithelium (Figure 15A); this invagination then deepens to form a cleft (Figure 15B). The

nascent shell forms at the surface of the cleft; as the shell develops, the shell field evaginates and spreads beneath it (Figure 15C) (Moor, 1983). After early morphogenesis, the tissue ventral and distal to the center of the shell becomes the outer mantle fold, while the tissue exterior and proximal to the margin of the shell becomes the middle mantle fold (Figure 15D; after Kniprath, 1977). The initial presence of a cleft with a narrow apical opening might provide mechanical support to the delicate layer of primordial periostracum which overlies the shell field (Moor, 1983). This periostracal layer both seals the shell field from the external environment and presumably serves as a matrix upon which calcification of the nascent shell is initiated.

In the teuthoid cephalopods, the gladius originates in a similar manner; the cleft however is not present (Bandel,



Explanation of Figures 11 to 14

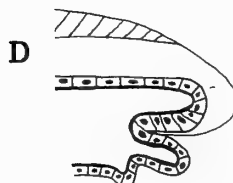
Figures 11–14. Detail of dorsal cells close to the longitudinal axis of the anterior part of the gladius in hatching *Loligo vulgaris*. Figure 11. Interdigitation of a muscle cell (MC) and a dorsal shell sac cell (DG) with the basal lamella (BL). Scale bar 0.2 μm . Figure 12. Myofibrils of a muscle cell (MC) converging on an insertion zone close to the basal lamella (BL) above the dorsal shell sac cells (DG). Scale bar 0.5 μm . Figure 13. Oval profiles of microtubules cut obliquely (OC). Scale bar 0.02 μm . Figure 14. Dorsal shell sac cells (DG) with microfilaments (MF) in cross section, close to the basal lamella (BL). Scale bar 0.2 μm .

1982) (Figure 15E, F). The shell field spreads as described above, but early in development, the tissue which is immediately exterior to the margin of the shell field, forms a ridge (Figure 15G), which then overgrows the shell field and fuses to form the shell sac (Figure 15H). The formation of a closed shell sac in squid takes place *prior* to development of the gladius; there is no “recapitulation” of an exposed shell stage in coleoid embryogenesis. Given the positional relationships among the different parts of the shell sac anlage, however, the dorsal layer of tissue (Figure 16B) can be considered homologous to the middle mantle fold of other mollusks, while the ventral layer is homologous to the outer mantle fold and mantle roof (Figure 16A) (Naef, 1928; Bandel & Boletzky, 1979; Pojeta, 1980).

Cytological features related to modifications of the periostracum: In bivalves and gastropods, the mode of formation of the periostracum varies among genera. The periostracum arises at the mantle edge, typically between the opposed membranes of the middle and outer folds of the mantle epithelium, which form a gutter, the periostracal groove (Figure 16A). The first layers of the periostracum originate at the base of the periostracal groove from cells which exhibit a unique morphology. These cells secreting the initial layers are usually referred to as basal cells when they form a simple monolayer, as in bivalves or periostracal gland cells when they form a more complex tissue, as in some gastropods. Regardless of the origin of the periostracum, it first appears as a layer of osmophilic

SHELL FIELD DEVELOPMENT

BIVALVE



CEPHALPOD



Figure 15

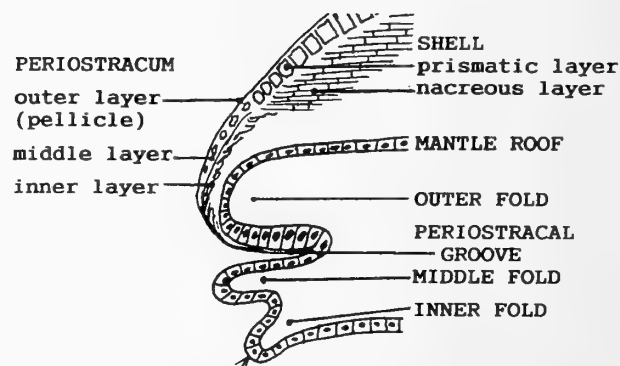
Comparative diagram of early development of the shell field in bivalves (A, B, C, D; after Kniprath, 1977) and in cephalopods (E, F, G, H). A: formation of a depression in the shell field; B: invagination with formation of the cleft; C: evagination of shell gland; D: mantle edge with developed mantle folds. E: central depression of shell field; F: spreading of shell field; G: formation of ridge, becoming elevated as a fold, around the shell field; H: closed shell sac.

material. The periostracum is commonly elaborated by additional layers applied to it within the periostracal groove, which are secreted by tissues of the outer and middle mantle folds that may exhibit diverse morphologies (Saleuddin & Petit, 1983; Neff, 1972; Bevelander & Nakahara, 1967; Kniprath, 1972).

In bivalves and gastropods, all or part of the periostracum is hardened by quinone tanning, forming an impermeable layer of sclerotized protein, which provides a barrier to the external medium protecting the shell from dissolution (cf. Isaji, 1993). In bivalves, there is good evidence that the periostracum serves as a site for nucleation of calcium carbonate crystals and deposition of the prismatic layer of the shell. It also serves as a base onto which layers of organic matrix are secreted, which are thought to provide the substratum for the nacreous layers of the shell in bivalves (Saleuddin & Petit, 1983; Bevelander & Nakahara, 1967).

As in bivalves, the ventral basal cells at the margin of the shell sac in *Loligo* (Figure 6), display a distinct mor-

BIVALVE MANTLE MARGIN



SQUID SHELL SAC

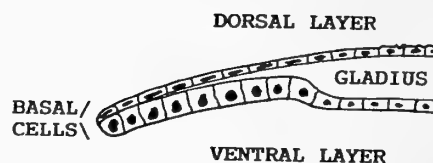


Figure 16

Diagrams of a generalized radial section of bivalve mantle margin with shell and posterior transverse section of the shell sac with gladius in *Loligo*.

phology from the cells adjacent to them. Examination of the base of the periostracal groove in the marine bivalve *Macrocallista maculata* (Bevelander & Nakahara, 1967) reveals that the initial periostracum is elaborated as a dense layer of osmophilic material between the opposed membranes of the basal cell of the outer fold and the adjacent cell of the middle fold of the mantle margin. In other bivalves, the periostracum can first appear as an osmophilic layer at the bottom of the periostracal groove (Saleuddin & Petit, 1983). In squid, no osmophilic layer is visible between the opposed membranes of the basal cells (Figure 6 inset), nor is osmophilic material detectable in the marginal gutter of the shell sac lumen where the fine edge of the gladius is first visible.

Morphological variation in shell forming epithelia: In the gastropods and bivalves, cells found in the folds of the mantle margin exhibit highly variable morphologies among genera. Because of this high variability, it is impossible to demonstrate homologies among cell types, but distinct zones of tissue with similar functions and morphologies are evident.

In bivalves, the tissue of the outer mantle fold proximal to the base of the groove is responsible for elaboration or modification of the periostracum. These are typically tall cells characterized by basal nuclei and extensive, rough endoplasmic reticulum with dilate cisternae; abundant golgi, apical microvilli, lysosomes, mitochondria, and dark granules, which contain mineralized material, are also commonly present (Saleuddin & Petit, 1983; Neff, 1972; Bevelander & Nakahara, 1967).

Calcium carbonate accretion is ascribed to the activity of the shorter cells located at the mouth of the periostracal groove and along the mantle roof. These cells often exhibit reduced endoplasmic reticulum, mitochondria, and other organelles associated with protein synthesis, as well as shorter microvilli (Saleuddin & Petit, 1983; Bevelander & Nakahara, 1967; Kniprath, 1972).

Cells of the middle mantle fold are flat or cuboidal with supposed functions related to elaborating, modifying, anchoring, and manipulating the periostracum out of the periostracal groove. These cells typically have sparse endoplasmic reticulum, and their microvilli are shorter than those found on the cells of the outer fold. They often display large electron-dense granules thought to contain enzymes such as phenoloxidase, instrumental in the quinone tanning process, and stout tegumental fibers (Bevelander & Nakahara, 1967; Saleuddin & Petit, 1983; Neff, 1972).

We show that distinct cell types are also found in the shell sac of the squid. Their morphologies and organization are similar to that of the cells found in the outer and middle mantle folds of other mollusks, particularly the bivalves.

In the ventral layer of the squid shell sac, which corresponds to the outer mantle fold, the cells proximal to the margin display most of the characteristics of the cells found proximal to the base of the periostracal groove. From their extensive rough endoplasmic reticulum and prominent golgi, we can infer that these cells are primarily responsible for the secretion of the materials that make up the gladius. One notable difference from bivalve tissue is that dark granules are not found in squid tissue. As these granules are thought to contain mineral material and to play some role in calcification, this comes as no surprise.

The cells lying close to the longitudinal axis of the gladius, which are reduced in height, appear to be secretory as well. The relatively low number of organelles responsible for protein synthesis might suggest that they contribute less to the overall bulk of the gladius, but Figures 3, 4 and 5 show that the thick rachis and its continuation into the anterior part of the vane is formed by these low cells, which appear to correspond to the distal cells at the "mouth" of the periostracal groove or mantle roof cells.

It is more difficult to make meaningful comparisons between the dorsal cells at the margin of the shell sac and the middle mantle fold cells because these cells do not exhibit many distinctive characteristics. The cells in both tissues are cuboidal with relatively short microvilli and little endoplasmic reticulum. Absent in the squid cells are the dark enzyme granules, which in bivalves are implicated in quinone tanning of the periostracum. If tanning is considered as a means of making the periostracum impermeable, it is not surprising that no tanning occurs in a completely sealed shell sac.

The dorsal cells in the shell sac found toward the longitudinal midline appear to play a role in anchoring the pen in the mantle. This is suggested by the bands of microtubules which extend diagonally from the interdigitated dorsal membrane; they fan out toward the microvillous ventral membrane. The bundles of microfilaments, the high degree of interdigitation with the basal lamella, and, in the case of the hatchlings, the insertion of muscle fibers opposite the interdigitated regions also suggest this. That these cells stain lightly and do not display prominent endoplasmic reticula or golgi indicates that they are not secretory.

Conclusion: The morphology and organization of the tissues which make up the shell sac in the squid are similar to those found in the outer and middle mantle folds of other mollusks, particularly the bivalves. However, it is notable that the organelles responsible for quinone tanning of the periostracum and the accretion of a calcified shell appear to be absent. Also absent are osmophilic layers of the nascent periostracum, typically found at the base of the periostracal groove in other mollusks. These observations, together with the developmental similarities in the shell field of mollusks derived from a "monoplacophoran" conchifer ancestor (Yochelson et al., 1973; Pojeta, 1980) suggest that homologues to the tissues making up the periostracal groove and the mantle roof in other mollusks are present in the squid shell sac. The absence of calcification must be due to "loss" of a special function which was once requisite to the original evolution of chamber formation in the cephalopod ancestor.

The above picture results from comparative analyses viewing the squid shell sac against the sepiid sac (and the *Nautilus* shell gland figured by Arnold, 1992). In taking the alternative view of constructional morphology, one will not so much underscore the loss of that special function as emphasize the *gain in plasticity* of the muscular mantle. Very fast swimming by jet propulsion could possibly be achieved *only in animals with elastic shells* when the mantle musculature remains in close contact with the shell sac. Similarly, loss of calcification could have opened the path toward differentiation of very elongate body forms adapted to macroplanktonic conditions. In both cases, one of the advantages of an elastic shell is that it can be bent when the body has to fold on itself, e.g., during defensive motor actions when the arms are used to free the mantle from a

would-be predator. This folding movement has been observed in early juvenile *Loligo vulgaris* (Boletzky, unpublished observation), but never in the subadults or adults of this species, which are characterized by very long fins. In contrast, shortfin squids are able to fold their mantle ventrally even at the adult stage (Boletzky, 1994).

It should be emphasized, however, that pinpointing these advantages is not meant to minimize the fact that the chambered shell design is clearly competitive in certain ecological contexts; that this design permits considerable morphological diversification is demonstrated by the sepiid cuttlefishes (see Nesis, 1987 for relevant literature).

ACKNOWLEDGMENTS

We would like to thank our colleagues and the technical staff of the Laboratoire Arago for their assistance in procuring materials and accessing the facilities. In particular, we would like to thank Dr. Marie Line Géraud for her assistance in utilizing the equipment and providing materials for the electron microscopy. We gratefully acknowledge M. V. v. Boletzky for the histological preparations on which Figures 1, 3, 4, and 5 are based.

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Ultrastructure of the Digestive Gland in the Opisthobranch Mollusk, *Runcina*

by

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Abstract. In the digestive gland of two *Runcina* species (*R. coronata* and *R. ferruginea*), four cell types have been identified: digestive cells, microtubule-containing cells, secretory cells, and mineral-containing granule cells. The digestive cells are the most numerous. Their apical brush border and the endocytotic vesicles indicate intensive uptake of food particles. A complex lysosomal system is responsible for breakdown, storage, and later expulsion of the degraded material into the gland lumen. The microtubule-containing cells exhibit voluminous endoplasmic reticulum cisternae filled with microtubules. Such microtubule-containing vacuoles have been described in ectodermal cells of *Runcina* and in other cephalaspids but not in the digestive gland. Their function is not known. The third cell type represents secretory cells. They produce large, spherical electron-dense secretory granules, which probably take part in extracellular digestion. Cells with birefringent, concentrically structured mineral-containing granules in their cytoplasm, seem typical for the digestive gland in most gastropods. The mineral composition varies among different species. In *Runcina*, the x-ray microanalytical spectrum reveals magnesium phosphate as the main component.

INTRODUCTION

The molluscan digestive gland develops from the endoderm. In the adult *Runcina*, the voluminous digestive gland constitutes a large part of the visceral mass and, together with the gonad, envelops the intestine. The digestive gland of *Runcina* consists of numerous lobules, which unite and open into the stomach. The digestive gland is also called the midgut gland, hepatopancreas, or liver. The latter two terms should be abandoned (Van Weel, 1974). The function of the molluscan digestive gland is thought to include the following functions: absorption of ingested food material, extracellular and intracellular digestion of food, excretion, osmoregulation, and secretion.

Structure and function of the digestive gland vary even within the same molluscan group. A table with a comparison of nomenclature used in older light-microscopical studies can be found in Schmekel & Wechsler (1968a). The cephalopods are not considered (see Schipp & Boletzky, 1975, 1976). Among gastropods, interest has mainly been focused on the structure of the digestive glands of pulmonates (Abolins-Krogis, 1963, 1965, 1970a, b, 1975, 1979; Sumner, 1966a–c; Reygrobellet, 1970; Walker, 1970; Arni, 1974) and bivalves (Sumner, 1966c, d; Owen, 1972;

Pipe & Moore, 1985). Some of the papers deal especially with shell repair. Within the opisthobranchs, sacoglossan species have attracted most of the attention because of their ability to retain “symbiotically” functional chloroplasts within the cells of the digestive tract (Taylor, 1968, 1971; Greene, 1970; Trench, 1969; Trench et al., 1973; Clark & Busacca, 1978; Clark et al., 1981; Graves et al., 1979; Griebel, 1993). Among nudibranchs, the aeolidiaceans develop specialized digestive cells within the cnidosacs at the tips of the cerata. They are able to store nematocysts for defense (Graham, 1938; Edmunds, 1966; Schmekel, 1972; Schmekel & Wechsler, 1968a, b; Kalker & Schmekel, 1976; Greenwood & Mariscal, 1984a, b). Little attention has been paid to cephalaspids. Only Fretter (1939) published a detailed light-microscopical account of the alimentary canal of *Philina aperta*, *Scaphander lignarius*, *Haminea hydatis*, and *Acteon tornatilis*, while Rudman (1971, 1972a–c) studied some New Zealand Bullomorpha (Cephalaspidea). No ultrastructural analysis of the digestive gland epithelium has so far been performed.

Runcina are shell-less cephalaspids which do not exceed 7 mm in length (Colosi, 1915; Burn, 1963). Two species occur in Plymouth Sound, *Runcina coronata* and *Runcina ferruginea* (for details see Kress, 1977, 1985a, b, 1986;

Kress & Schmekel, 1992). Features of the epithelial cells lining the digestive lobules and their possible function are covered in the present study. Because there is no noticeable variation related to animal size or to species, the two species will be described together.

MATERIALS AND METHODS

Specimens of *Runcina coronata* (Quatrefages, 1844) were collected from coralline rock pools near the upper littoral fringe in Plymouth Sound. *Runcina ferruginea* (Kress, 1977) breed successfully in aquaria at the Plymouth Marine Biological Laboratory.

Light Microscopy

Specimens from 1 to 7 mm in length were fixed in the solutions of Bouin, Helly, and Petrunkewitch, embedded in Paraplast, and stained with Pasini, PAS, and May-Grünwald-Giemsa.

Electron Microscopy

Pieces of tissue were placed in one of the following fixatives:

- (a) 2.5, 3, or 5% glutaraldehyde in seawater.
- (b) 2.5, 3, or 5% glutaraldehyde in 0.1 M or 0.2 M sodium cacodylate buffer.
- (c) 3% glutaraldehyde in 0.1 M sodium cacodylate buffer with 25% sucrose and 0.5% CaCl_2 at pH 7.2–7.4 (Coggeshall, 1972).
- (d) 1% OsO_4 in seawater.
- (e) 1% OsO_4 in 0.1 M sodium cacodylate buffer.
- (f) Addition of 0.05% OsO_4 to the glutaraldehyde fixative according to the method of Eisenman & Alfert (1982).

The tissue was fixed for 2 hr or longer, at 4°C, then rinsed overnight in seawater or sodium cacodylate buffer. Postfixation took place in 1% OsO_4 in seawater or 0.1 M sodium cacodylate buffer for 1–2 hr at 4°C. The tissue was dehydrated through an acetone series and embedded in Epon 812. Semithin (1.5 μm) sections were cut and stained with 1.4 phenylene diamin. Thin sections were cut on a Reichert OMU2 ultramicrotome and mounted on copper grids. They were stained with uranyl acetate and lead citrate and examined with a Philips 301 electron microscope.

Fixatives (c) and (e) produced the best results, although the others revealed interesting additional aspects.

To delineate the cell boundaries and study the possible uptake of material, the lanthanum nitrate method was applied. The tissue was immersed for 1 hr in a fixative prepared from equal volumes of 6% glutaraldehyde in either 0.09 M S-collidin buffer or seawater with the addition of 2% lanthan nitrate. Tissues were postfixated in 1% OsO_4 in 0.1 M sodium cacodylate for 1 hr.

For x-ray microanalysis, the digestive glands were dissected out and smeared thinly on graphite scanning electron microscope (SEM) specimen stubs and air dried. The

stubs were viewed for mineral granules, which were imaged by backscatter electron detection. Individual granules were probed with a stationary spot at 25 kV, and elemental spectra were produced by energy dispersive x-ray microanalysis.

RESULTS

Anatomy

The buccal cavity contains a tricuspidate radula (1.1.1) of about 20 rows and lubricating glands lining the cavity and oral canal, including a pair of salivary glands. The esophagus leads to a muscular gizzard which contains four plates with transverse ridges and opens into a thin-walled stomach. It is accompanied by digestive gland lobes which are divided into lobules. Colosi (1915) described several subdivisions of these lobes in *Runcina calaritana*. The intestine leaves the stomach dorsally forming a loop and runs between the digestive gland to the anus, which is placed a little to the right of the midline, opening into the mantle groove. The intestine is heavily ciliated. The fresh digestive gland is generally yellowish-brown or black as described for *Metaruncina setoensis* by Baba (1967).

Histology

The wall of the digestive gland is, depending on its functional state or the amount of food passing, more or less bulging. The single-layered epithelium is separated from the surrounding connective tissue and muscle cells by a basal lamina of varying thickness. The epithelial cells of the digestive gland are variable in height and shape. Intercellular space is narrow, and interdigitations between the cells occur basally. Apically, desmosomes are visible. Controversy exists about the possible number of cell types taking part in the different functions assigned to the digestive gland, about the nature of the different inclusions, and the homology of given names in the different groups of gastropods (Schmekel & Wechsler, 1967; Schmekel, 1979; Owen, 1972).

In *Runcina*, four types of cells are identified within the digestive gland epithelium, together with basally situated stem cells and occasional mucous cells and ciliated cells.

Here the four cell types are described: digestive cells, microtubule-containing cells, secretory cells, and mineral-containing granule cells (Figure 1a–e).

Description of the Four Cell Types

Digestive cells (Figures 1a, b, 2–11, 23a): This is the most abundant cell type in the digestive gland. The cells are variable in shape and size (Figures 1a, b, 2, 3). Many appear cuboidal or cylindrical, but in general, they are narrow at the base, have a long club-shaped upper part, and bulge into the lumen. The height varies from 45 to 88 μm . Apically the cells carry slender microvilli (Figure 4). Along the base of the microvilli, there is a terminal

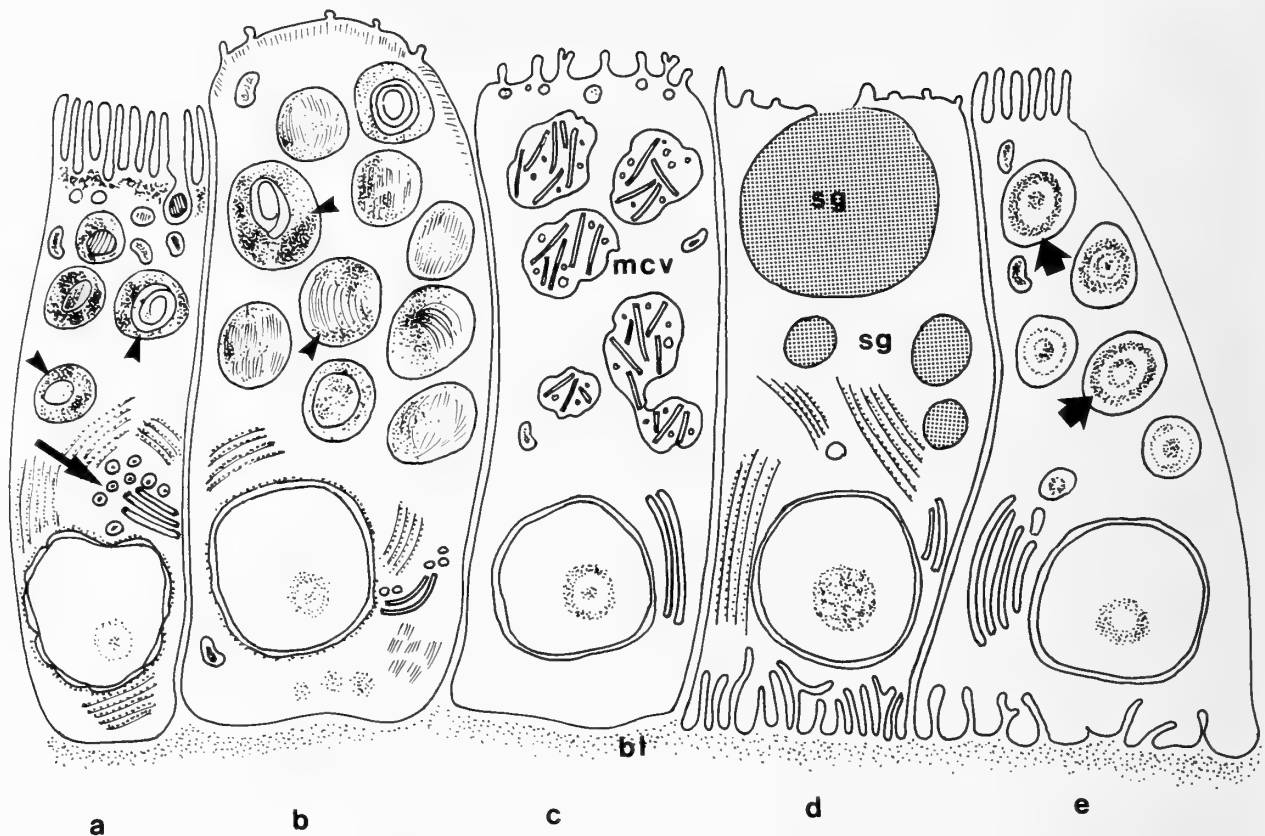


Figure 1

Diagram illustrating the ultrastructural organization of epithelial cell types in the digestive gland of *Runcina*. a, b) Digestive cells; a) a cell showing active endocytosis and containing primary- and heterolysosomes, b) a cell congested with heterolysosomes, residual bodies, and lipid droplets; c) microtubule-containing cell; d) secretory cell; e) mineral-containing granule cell with concentrically structured membrane-bound granules. Primary lysosomes (arrows), heterolysosomes (arrow-heads), microtubule-containing vesicles (mcv), secretory granules (sg), concentric arrangement of material in the mineral-containing granules (broad arrows), basal lamina (bl).

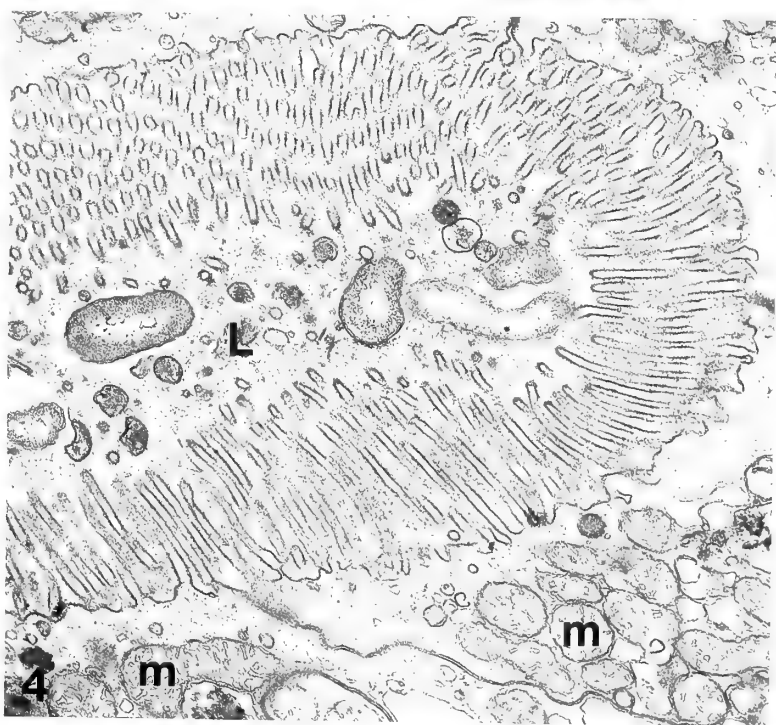
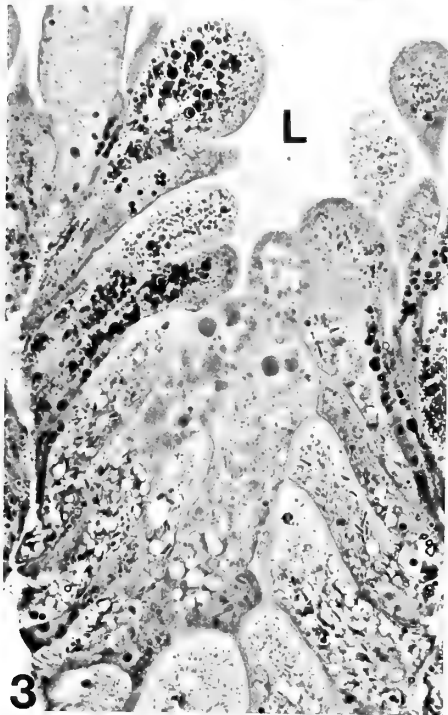
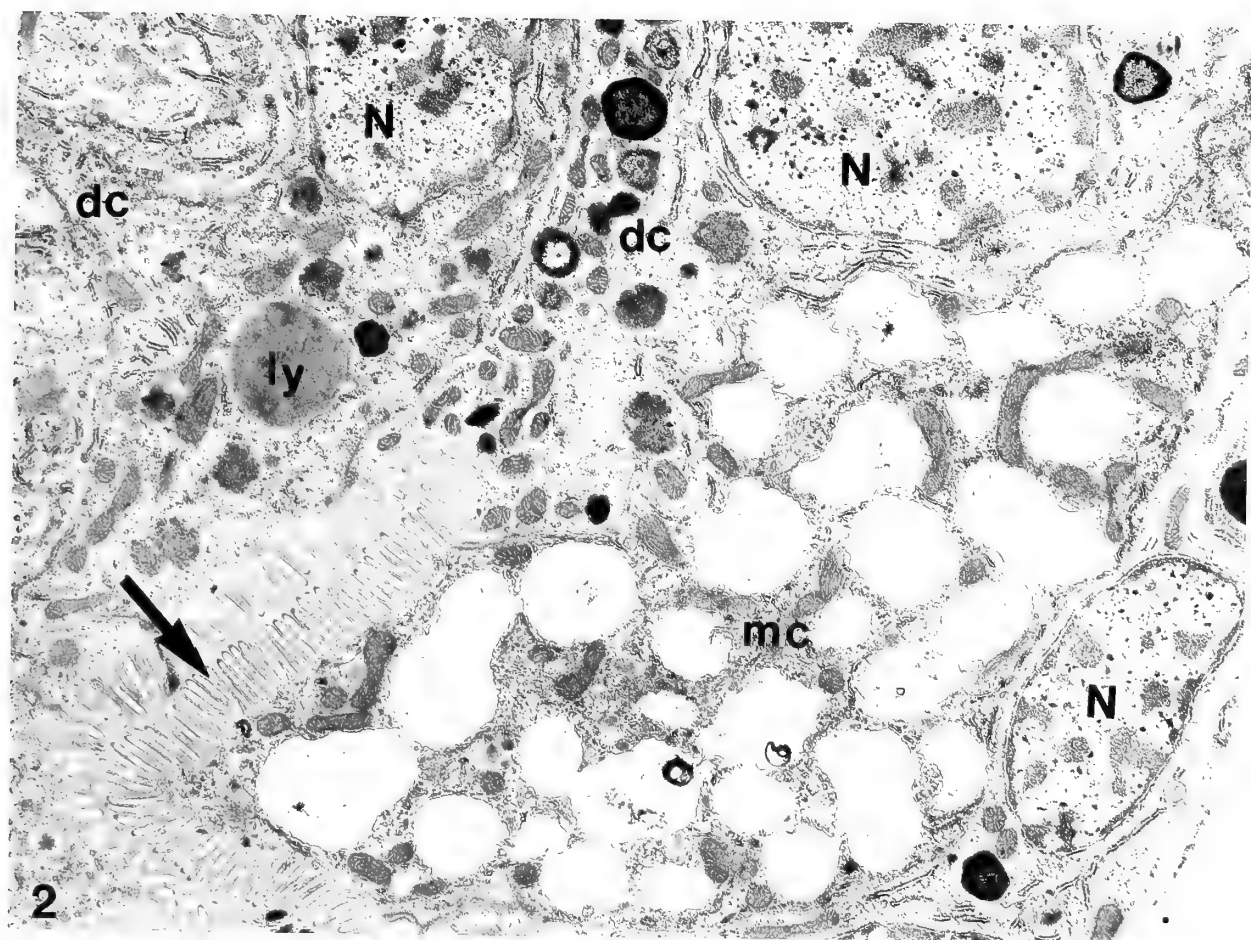
web, and endocytotic vesicles are regular features (Figure 5). The plasma membrane at the cell base has slight undulations but no labyrinth. The lateral walls show only a few interdigitations. The nucleus is round or ellipsoid in outline, sometimes indented, and has a distinct nucleolus. The outer nuclear membrane exhibits numerous pores and carries ribosomes. Rough endoplasmic reticulum and Golgi complexes are abundant, and the formation of electron-

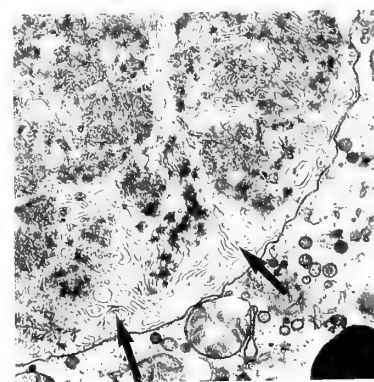
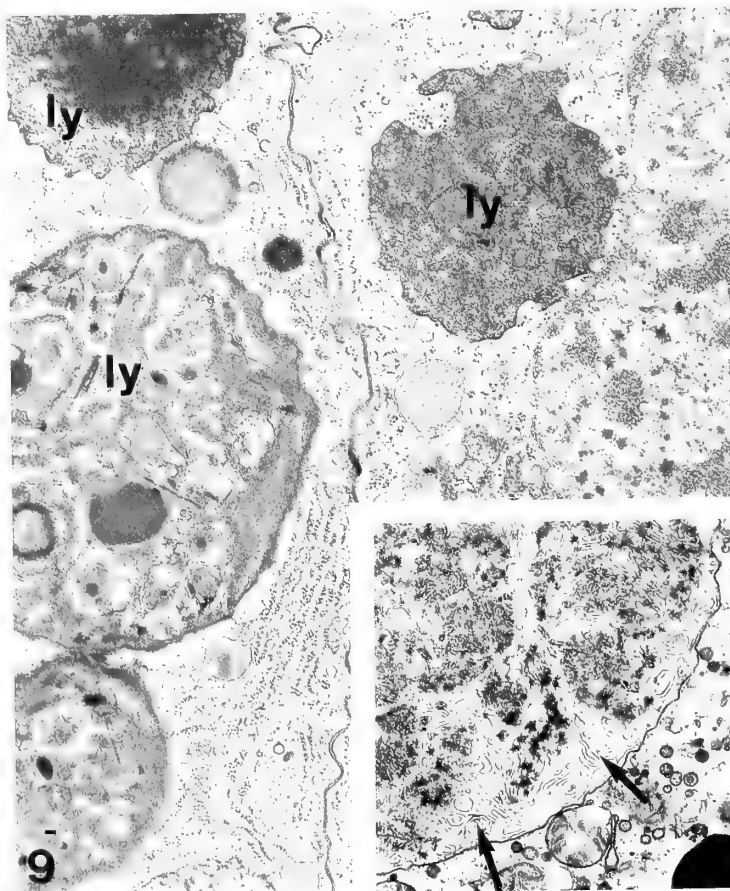
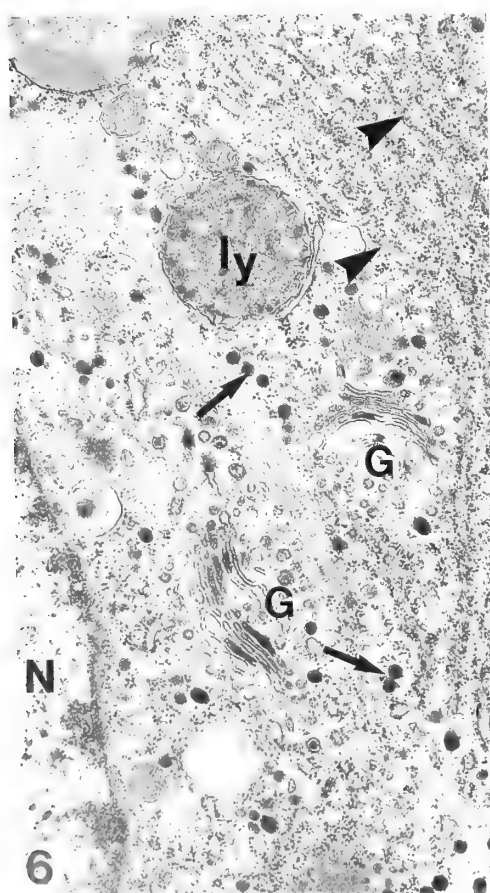
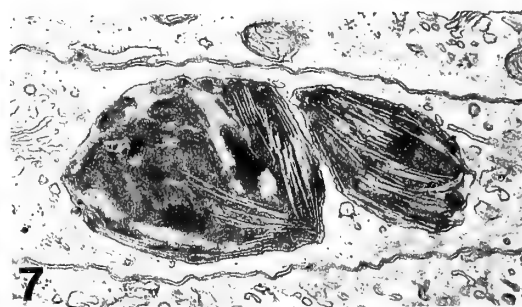
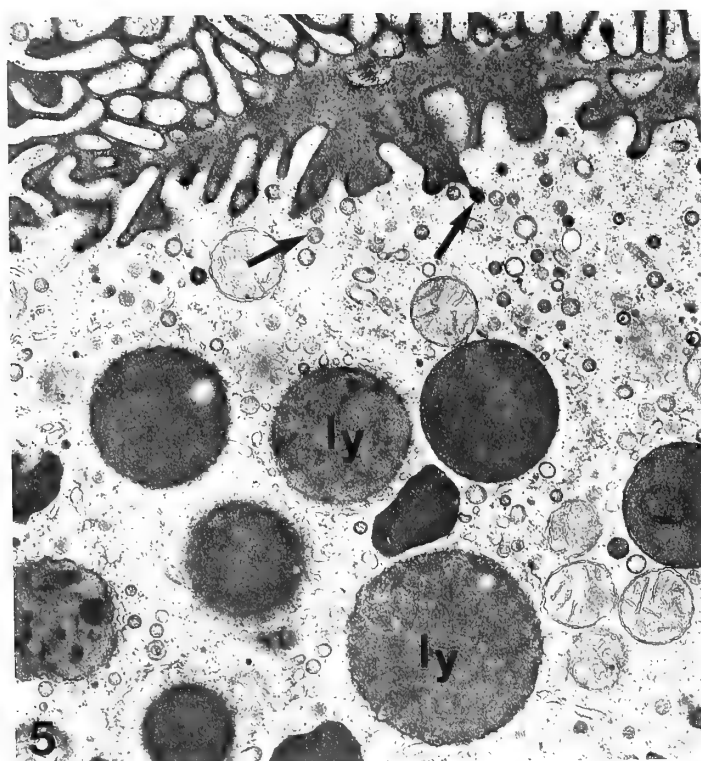
dense primary lysosomes is visible (Figure 6). Mitochondria are especially numerous in apical areas.

In the light-microscope, especially on semithin sections, the cytoplasm appears filled with darkly stained granules and/or vacuoles of different sizes (Figures 3–11). The electron microscope reveals that the digestive cells show intensive uptake of food particles and some remnants, presumably of chloroplasts (Figures 5, 7). The material is

Explanation of Figures 2 to 4

Figure 2. Micrograph of digestive cells (dc) with an interspersed mucocyte (mc). The digestive cells resemble type a in the diagram (Figure 1) and carry a dense brush border. Glandular lumen (arrow); nucleus (N); lysosomes (ly). $\times 8600$; Figure 3. Semithin section through part of the digestive gland wall with predominant digestive cells of balloonlike appearance. According to the stage of intracellular digestion, size and density of granules and vacuoles vary considerably. Lumen (L) $\times 480$. Figure 4. Food particles in the digestive gland lumen (L), consisting of the remnants of bacteria, unicellular algae, and detritus. The adjacent digestive cells carry a dense brush border and exhibit numerous mitochondria (m) in the apical cytoplasm. $\times 15,000$.





found in heterolysosomes which can also contain membrane whorls and myelinlike structures and have the appearance of residual bodies (Figures 5, 8, 9, 10). Their diameter is up to $3.5\text{ }\mu\text{m}$. The frequency of heterolysosomes depends on the functional state of the cell. The x-ray microanalysis of the lysosomes in the digestive cells produces spectra with major peaks for sulphur, phosphorus, and chlorine; and minor peaks for potassium, calcium, magnesium, and sometimes iron and zinc (Figure 23a). These vacuoles are extruded into the gland lumen, where putative waste occurs regularly. Generally, digestive cells which expel material have an irregular apical outline and fewer microvilli, and the process of extruding excretory matter is often comparable with apocrine secretion. Between the heterolysosomes, there are fatty droplets and glycogen particles. The activities of neighboring digestive cells are not synchronized, and different stages of uptake and breakdown of food can be observed simultaneously. In digestive cells, there are occasional microtubule-containing vacuoles, but no mineral-containing granules.

Microtubule-containing cells (Figures 1c, 11–14): In many respects, the microtubule-containing cells resemble digestive cells. They bulge into the gland lumen and are about $60\text{ }\mu\text{m}$ in height. However, they contain large colorless vacuoles (Figure 11). The apical plasmalemma exhibits irregularly spaced, sometimes even forked, microvilli. Endocytotic processes are conspicuous (Figure 12). No basal labyrinth is formed. The position of the nucleus within the cell is highly variable. The nucleus is often filled with a network of heterochromatin and has a distinct nucleolus (Figure 11). The outer nuclear membrane is devoid of ribosomes. Mitochondria are small and rather scarce. The endoplasmic reticulum is dilated into irregularly shaped cisternae, many of which contain fine, flocculent material. In many of them, however, there are accumulations of microtubules of about 30 nm in diameter (Figure 12). They may be irregularly spaced, sometimes oriented in parallel. The cisternae or vesicles measure up to $3.5\text{ }\mu\text{m}$ in diameter. In more mature cells, the density of microtubule packing increases, and the vesicles and vacuoles contain more osmiophilic material, which is sometimes of crystalloid appearance (Figures 13, 14). Microtubules or densely packed material in the vesicles are

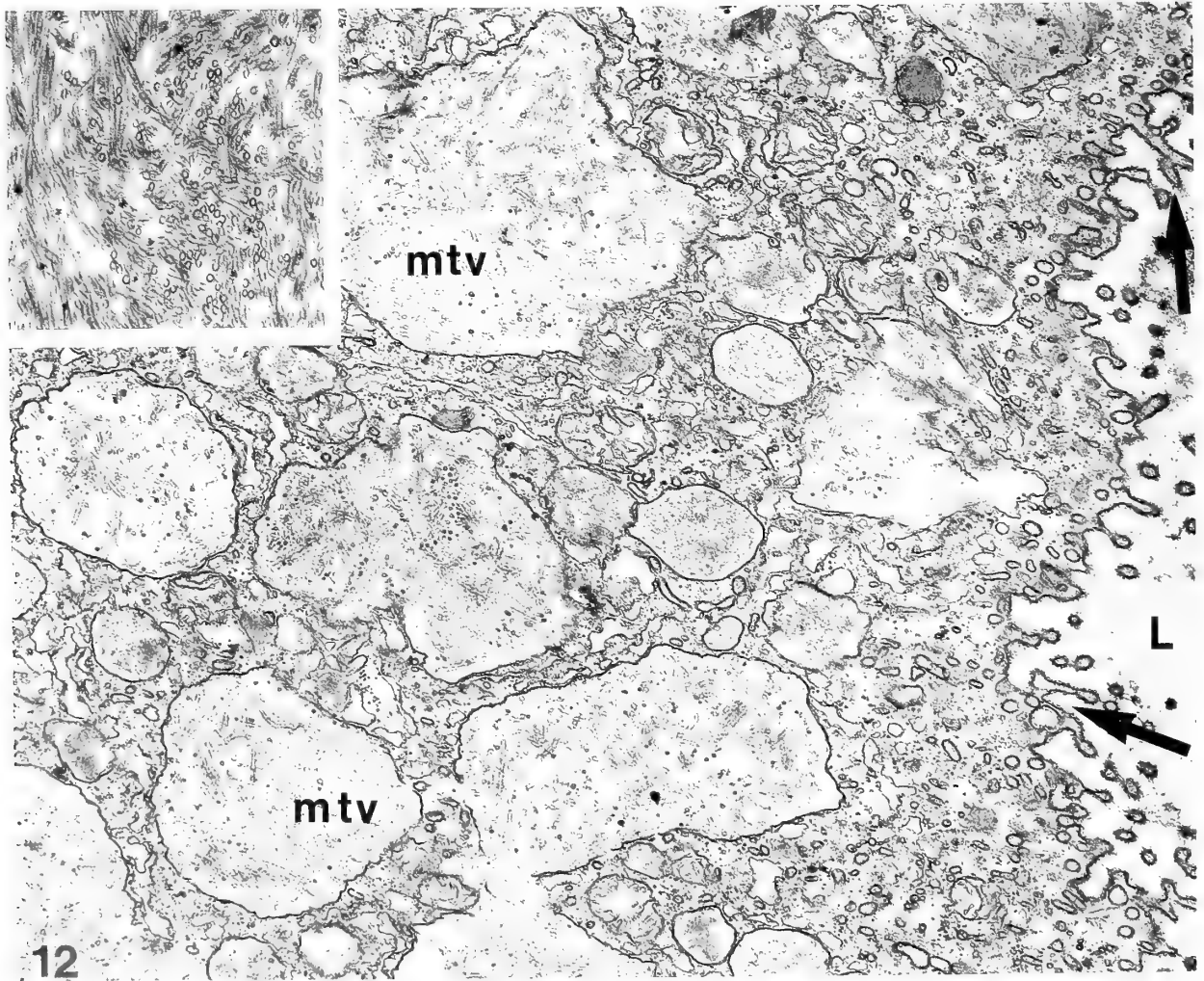
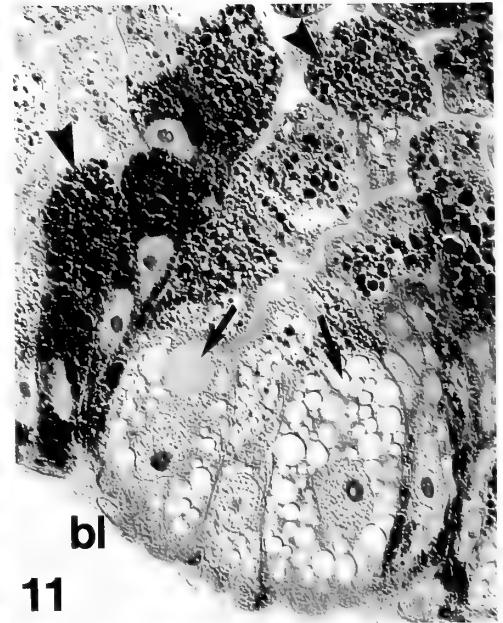
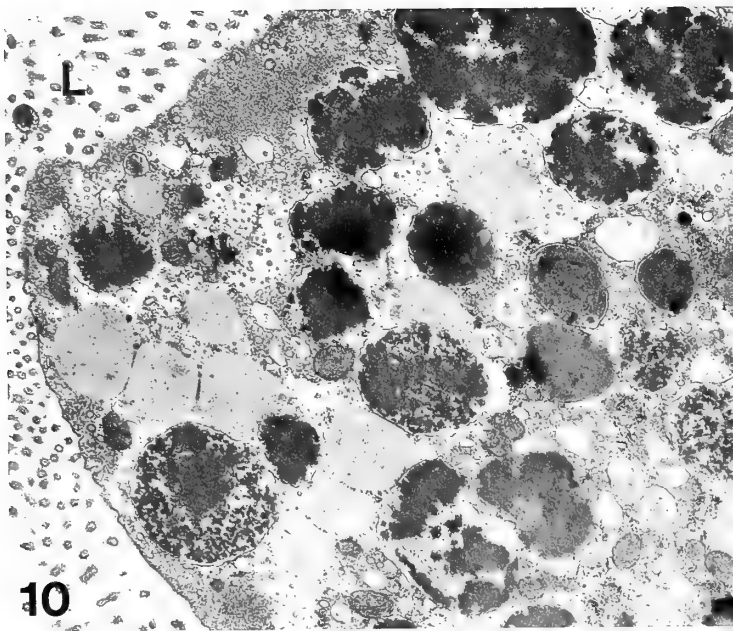
apparently expelled into the gland lumen, where they can be detected. In microtubule-containing cells, there are no heterolysosomes similar to those seen in the digestive cells, but there are occasional mineral-containing inclusions.

Secretory cells (Figures 1d, 15–17): The secretory cells are often of roughly triangular shape, slightly bulging, and up to $60\text{ }\mu\text{m}$ in height. In the semithin sections, a few electron-dense granules are visible in the apical part of the cells (Figure 15). The apical border carries irregularly arranged short microvilli. The cells possess a conspicuous basal labyrinth (Figure 16). The spherical nucleus includes a netlike nucleolus, and the outer nuclear membrane carries ribosomes. There is a well-developed rough endoplasmic reticulum but only a small Golgi apparatus. The cytoplasm contains large, electron-dense, spherical inclusions, enveloped by a membrane, sometimes up to $7\text{ }\mu\text{m}$ in diameter. They probably are secretory products, which are released into the digestive gland lumen as part of a system of extracellular digestion (Figure 17). In these secretory cells, there are no mineral-containing granules and no distinct heterolysosomes.

Mineral-containing granule cells (Figures 1e, 18–22, 23b, 24): The cells containing the biomineralized granules are pyramidal in shape with the broad base exhibiting a basal labyrinth, i.e., a large surface for exchange processes with the haemolymph. The apical surface is formed by a brush border of slender microvilli (Figure 18). While in younger cells the nucleus is more centrally located, it is later shifted toward the base of the cell when the number of granules increases. The nuclear membranes are often dilated, but do not carry ribosomes. Little glycogen, few lipid droplets, small heterolysosomes, and distinct Golgi complexes are found in the cytoplasm. The rough endoplasmic reticulum is abundant and forms long strands or irregularly shaped cisternae (Figure 19). It is associated with the first stages of formation of the mineral-containing granules (Figure 19). Depending on the method of fixation and the plane of section, these granules are more or less concentrically structured and isolated within the cytoplasm by a limiting membrane (Figures 19–21). In semithin sections, these granules appear as birefringent structures (Figure 22).

Explanation of Figures 5 to 9

Figure 5. Section through the apical cytoplasm of a digestive cell. It reveals endocytotic vesicles (arrows) and an accumulation of secondary or heterolysosomes (ly). Lanthan nitrate method. $\times 17,800$; Figure 6. Active digestive cells with an extensive rough endoplasmic reticulum (arrow heads), and Golgi fields (G) taking part in the formation of primary lysosomes of varying density (arrows). Nucleus (N); heterolysosome (ly). $\times 17,100$; Figure 7. Digestive cells with the remains of chloroplasts. $\times 27,000$; Figure 8. Portion of a digestive cell where engulfed food particles can be identified in a heterolysosome (arrow) $\times 13,200$; Figure 9. Micrograph of digestive cells illustrating the variety of heterolysosomes (ly) due to the degradation and intracellular digestion of food components. $\times 17,800$; Inset: Detail of a lysosome containing whorls and remnants of membranes (arrows) $\times 13,200$.



In SEM, granules from the digestive gland of *Runcina* appeared as dense spheres up to 10 μm in diameter (Figure 24). In the x-ray microanalytical spectrum, major peaks appeared for magnesium, phosphorus, and potassium, and minor peaks for sulphur and chlorine (Figure 23b). Occasionally there were small peaks for zinc and calcium. These spectra indicate that the granules consist mainly of magnesium phosphate. The analysis of fixed material revealed the nearly complete loss of magnesium, potassium, and chlorine. Under the light microscope, the concentric structured granules make the cell look colorless but filled with refringent concentric markings. The magnesium phosphate granules are expelled into the digestive gland lumen and become part of the fecal material.

Amoebocytes have not been found accumulated near the digestive gland, and whether "Blasenzellen" play a role in digestion, uptake, or transport of food material in *Runcina* is not known (Fretter, 1939; Forrest, 1953; Buchholz et al., 1971; Abolins-Krogis, 1972; Schmekel, 1972).

DISCUSSION

Runcina lives predominantly on coralline flats where it finds sufficient amounts of small green algae, bacteria, and detritus for its food requirements. Occasionally, some chloroplasts occur within digestive cells.

The secretion from the salivary glands lubricates the food and may start preliminary digestion. In the carnivorous cephalaspids *Philine* and *Scaphander*, the secretion contains various enzymes such as amylase, glycogenase, lipase, and protease (Fretter, 1939). The runcinid gizzard with its plates forms a very effective grinding mill, insuring fragmentation of the food. Digestion of the food continues in the stomach to produce finely fragmented and semifluid materials; this chyme is conveyed by a combination of muscular and ciliary action to the digestive gland for absorption, further extracellular digestion, intracellular digestion, and formation of waste products (Thompson, 1976).

At the ultrastructural level, the cephalaspidean digestive gland, as represented by the two species of *Runcina* studied here, has four distinct cell types, not including stem cells and the occasional mucous cells. These types are the digestive, microtubule-containing, secretory, and mineral-containing granule cells.

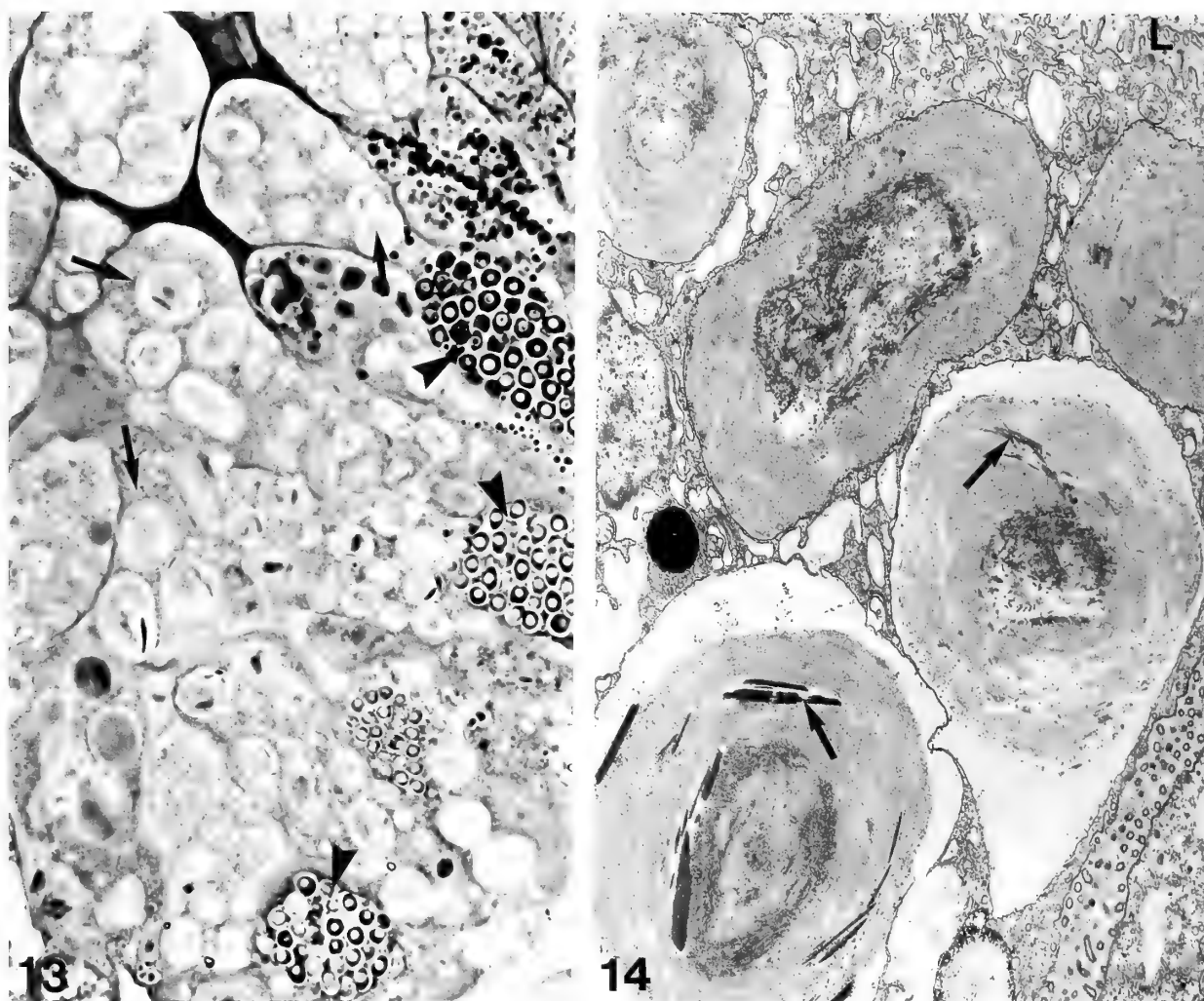
Among gastropods, the epithelial cells of the digestive gland appear highly variable in shape, in size, and in

staining qualities, due to the variety of diets, the changes occurring in the food during biochemical breakdown, and the different storage products. Taking all that into consideration, it is not surprising that at the light-microscopical level, this has led to an intensive discussion about how many cell types take part in food processing in opisthobranchs. The numbers given vary from one in *Tritonia hombergi* (Thompson, 1976), two in *Haminea hydati* and *Haminea zelandica* (Fretter, 1939; Rudman, 1971, 1972a; Thompson, 1976), three in *Aceton tornatilis* and *Philine aperta* (Fretter, 1939), *Metaruncina setoensis* (Baba, 1967), *Philine angasi*, *Aglaja cylindrica* (Rudman, 1972a, b), *Archidoris pseudoargus* (Forrest, 1953), *Elysia viridis* (Griebel, 1993), *Peltodoris atromaculata* (Fournier, 1969) to four in *Scaphander lignarius* (Fretter, 1939), and *Goniodoris* (Forrest, 1953). Some authors include stem cells in the number of cell types (Forrest, 1953; Arni, 1974; Schmekel & Wechsler, 1967; Walker, 1970). The same problem arises with the counting of mucocytes as entities among the different epithelial digestive cells. Some authors count mucocytes among them; other authors take a different view (Arni, 1974; Schmekel & Wechsler, 1967; Griebel, 1993).

Digestive cells form the main bulk of the epithelial cells lining the digestive gland lumen. They are of similar structure in all gastropods and bivalves investigated so far. Soon after digestion begins, food particles are taken up by endocytosis for intracellular breakdown, and food vacuoles can be seen in histological sections. In those species for which the food is known, it can be identified in various stages of decomposition within the lysosomal system. Among opisthobranchs, special attention has been paid to the sacoglossans because of their ability to retain symbiotically functional chloroplasts within their digestive cells. *Codium* chloroplasts have been described in *Elysia viridis* and *Tridachia crispata* (Taylor, 1968; Trench, 1969; Trench et al., 1973; Greene, 1970; Griebel, 1993), *Vaucheria* chloroplasts in *Elysia chlorotica* and in *Alderia modesta* (Graves et al., 1979), and *Halimeda* chloroplasts in *Bosellia mimetica* (Schmekel, personal observation). Aeolids feeding on hydroids are known to store whole nematocysts in the digestive cells, especially in the cnidosac in the tips of the cerata, probably for defense purposes (Edmunds, 1966; Schmekel & Wechsler, 1967; Kalker & Schmekel, 1976; Greenwood & Mariscal, 1984a, b). The digestive cells of the lower region of the midgut gland phagocytose and digest hydroid material, even some nematocysts. Such pro-

Explanation of Figures 10 to 12

Figure 10. Digestive cell, similar to Figure 1b, densely packed with heterolysosomes and residual bodies. Lumen (L) $\times 10,400$; Figure 11. Semithin section in Nomarski contrast revealing the different appearance of digestive cells (arrow heads) and microtubule-containing cells, the latter with large, apparently empty vacuoles (arrows). Basal lamina (bl). $\times 600$; Figure 12. Micrograph of a microtubule-containing cell. Note the irregularly shaped and forked microvilli (arrows) and the numerous vesicles or vacuoles filled with randomly orientated microtubules of varying length (mtv). Lumen (L) $\times 17,800$; Inset: Detail of microtubules $\times 29,000$.



Explanation of Figures 13 and 14

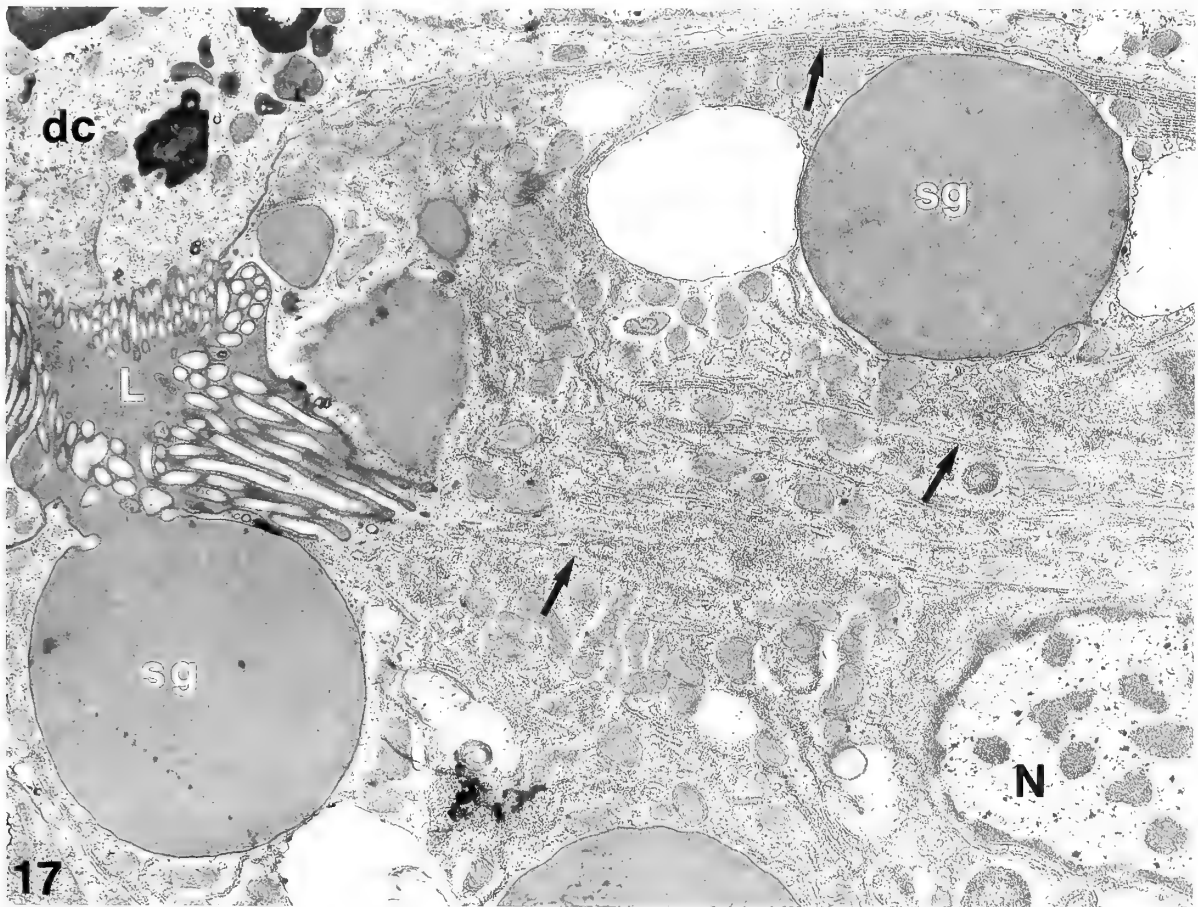
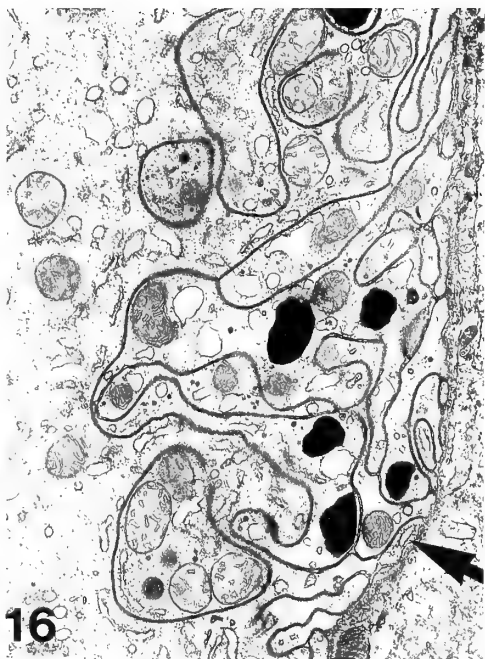
Figure 13. Semithin section through the digestive gland epithelium exhibiting microtubule-containing cells (arrows) and mineral-containing granule cells (arrow heads). Many vesicles in the microtubule-containing cells contain dense particles as depicted in Figure 14. $\times 640$; Figure 14. The microtubule content within the vesicles becomes more densely packed, and zones which resemble crystalloid structures appear (arrows). Gland lumen (L.). $\times 7800$.

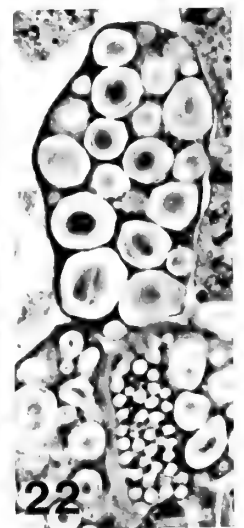
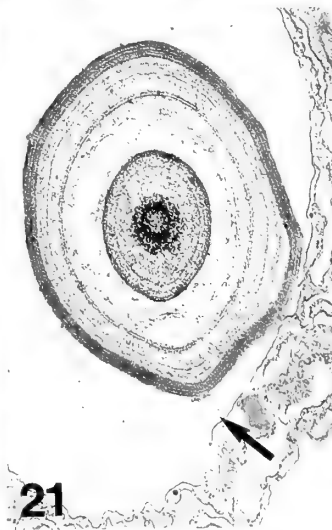
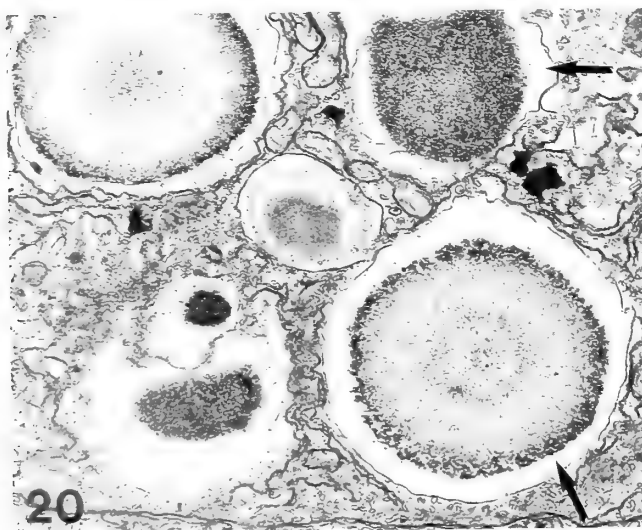
cesses have been described from *Podocoryne* in *Cuthona granosa* (Schmekel & Wechsler, 1967) and from many other hydroids in eolids e.g., *Eudendrium* in *Facelina* and *Cratena peregrina* (Kälker & Schmekel, 1976).

The digestive cells of *Runcina* are characterized by an extensive lysosomal system, similar to that described for *Cuthona* (Schmekel & Wechsler, 1968a) and *Mytilus* (Pipe & Moore, 1985). The membrane-bound bodies represent

Explanation of Figures 15 to 17

Figure 15. Semithin section in Nomarski contrast depicting secretory cells with dark spherical secretory granules (arrows). In the lower left-hand corner, mineral-containing granules appear as intracellular birefringent, concentrically arranged structures (arrow heads). $\times 800$; Figure 16. Basal portion of a secretory cell with conspicuous invaginations and interdigitations of the plasma membrane. Basal lamina (arrow) $\times 9900$; Figure 17. Secretory cell with large secretory granules (sg), one of which is continuous with the digestive gland lumen (L). Digestive cell (dc), nucleus (N), rough endoplasmic reticulum (arrows). $\times 8600$.





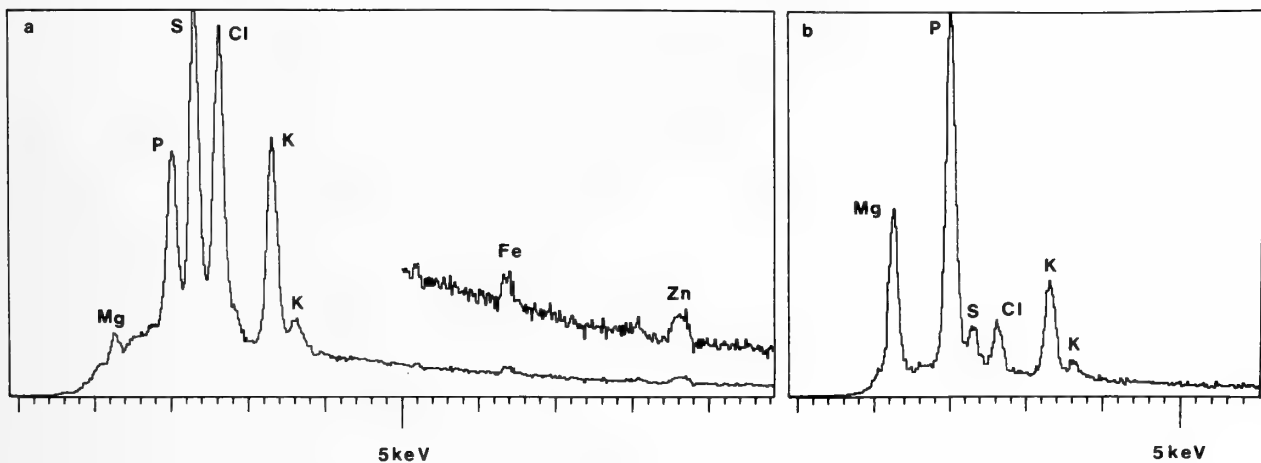


Figure 23

X-ray microanalytical spectra produced by 25 kV beam focused as stationary spot in the SEM. Horizontal scale: x-ray energy in keV; Vertical scale: x-ray counts. a) Analysis of lysosomes in digestive gland tissue. b) Analysis of a magnesium phosphate granule in digestive gland tissue squashed on a graphite stub.

heterolysosomes and residual bodies. Within the vesicles, the lysosomally mediated catabolism leads to a great variety of structures. The lysosomes have a dual function; they provide the molecular metabolic resources, and they return the residual waste matter to the lumen of the digestive gland. It is known that in many invertebrates lysosomes are able to accumulate heavy metals such as iron, zinc, or copper in non-toxic form within lysosomes and thus represent a second detoxification mechanism beside mineral-containing granules (Viarengo & Nott, 1993). Traces of iron and zinc have been found in digestive cell lysosomes in *Runcina*. The fecal matter is bound up by mucus, transported to the stomach, and from there, to the intestine. Old digestive cells are filled with lysosomes; they may undergo apoptotic changes and are eliminated. A digestive pattern as described for aeolids by Graham (1938) was not observed in *Runcina*; also no breakdown of food by amoebocytes as described by Fretter (1939) and Forrest (1953) was observed.

Fretter (1939) studied the site of food absorption in cephalaspids by feeding the animals with insoluble iron saccharate, carmine, or algae; McLean & Holland (1973)

added ferritin to the prey of *Nassarius*. In both cases, the uptake of the material in question into digestive cells could be traced. Such specialized feeding experiments have not been done with *Runcina*.

Microtubule-containing cells have not yet been described as a special epithelial cell type in any molluscan digestive gland. The cells with dilated rough endoplasmic vesicles which contain microtubule material were found in *Runcina* specimens fixed by a variety of methods; they therefore cannot represent an artifact. The microtubule content is emptied into the digestive gland lumen by exocytosis, where it can be detected in some cases. It has been speculated that microtubules act as a sort of glue to form the fecal products, but the function of these microtubules remains enigmatic. In the mantle groove of *Runcina*, Peters (1993) found cells filled with vacuoles in which microtubules had accumulated before being expelled to the surface. In the ectodermal mantle groove, these extruded microtubules may assist in protecting the sensory epithelia.

In *Lymnaea*, Fain-Maurel (1969a, b) described "grains de sécrétion à microtubules" in the salivary gland, and Stang-Voss & Staubesand (1971) found accumulated microtu-

Explanation of Figures 18 to 22

Figure 18. Apical region of a mineral-containing granule cell, with brush border and two granules. Lumen (L). $\times 15,000$; Figure 19. Lateral region of a mineral-containing granule cell, depicting stages during formation of the concentrically structured granules. They originate and mature in the cisternae of the endoplasmic reticulum (arrows). The empty spaces around the granules indicate shrinkage and a possible loss of material during fixation. $\times 14,300$; Figures 20, 21. These pictures confirm the formation of mineral-containing magnesium phosphate granules within the endoplasmic reticulum (arrows). The different appearance results either from loss of material during fixation, shrinkage of the surrounding tissue, or it is due to the plane of section through the granules. $\times 9000$, $\times 15,500$; Figure 22. Semithin section showing a mass of magnesium phosphate granules within a cell. $\times 640$.

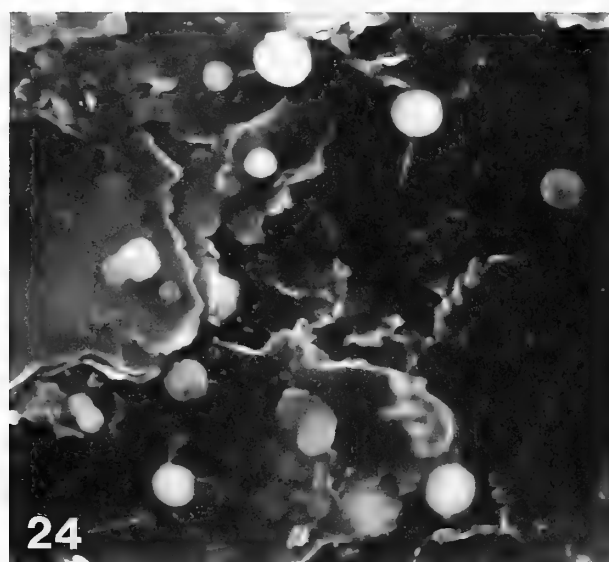


Figure 24

Magnesium phosphate granules as they appear in digestive gland tissue smeared on a graphite stub and viewed in the SEM. $\times 4400$.

bules in the cisternae of the granular endoplasmic reticulum of connective tissue cells. The authors assumed that the microtubules exhibited an intermediate stage of cellular synthesis, showing temporarily the pattern of a structural protein. In *Arion ater*, a "spongy layer" built from microtubules arranged between the microvilli of sensory epithelia of the tentacles has been depicted (Wright, 1974a, b). Similar pictures of microtubules produced by sensory and supporting cells are described in the organ of Hancock in the cephalaspidean genera *Scaphander* and *Haminea* (Peters, 1993).

The "lamellar" material mentioned for some veliger types of planktonic gastropods by Bonar (1978), Bonar & Mangel (1982), and Fiege (1990) seems to differ from microtubules.

Secretory cells like those found in *Runcina* have been described only in bivalves (Sumner, 1966c; Owen, 1972). In the bivalves, these cells look similar to those of protein secreting cells of the mammalian pancreas: pyramidal in shape with a well-developed rough endoplasmic reticulum and large membrane-bound secretory granules. In *Runcina*, exocytosis of similar looking secretory granules, probably containing digestive enzymes, can be demonstrated.

In some pulmonates, putative secretory cells have been described (Walker, 1970; McLean & Holland, 1973; Arni, 1974). These cells resemble stem cells, possess a great number of free ribosomes, and are of basophilic appearance. Owen (1972), however, distinguished between these basophilic stem cells and the above mentioned basophilic secretory cells.

Another digestive cell type so far found only in *Cuthona granosa* and *Elysia viridis* is characterized by a specially

formed border of microvilli (Schmekel & Wechsler, 1968a; Griebel, 1993). In *Cuthona*, the microvilli are connected with each other, and between the bases of the microvilli, intensive micropinocytosis takes place. These cells seem not to be able to phagocytose. They increasingly store residual bodies with age. This pigment can be seen through the ectoderm and contributes to the color of the animal. The cerata of young specimens are still greyish-white, while the cerata of old specimens appear black.

Mineral-containing granule cells: Species from many invertebrate phyla possess the ability to form intracellular mineral deposits in the form of spherical, concentrically structured membrane-bound granules. Among mollusks, they are well known in many pulmonates (Abolins-Krogis, 1963, 1965, 1970a, b, 1975), in all opisthobranchs (Taylor, 1968; Schmekel & Wechsler, 1968a, b; Griebel, 1993) and in many prosobranchs (Mason & Nott, 1981). The digestive gland appears to be one of the prime sites for mineral storage (Simkiss, 1976; Brown, 1982).

The granule cells in *Runcina* are predominantly situated in cryptlike structures of the digestive gland. They have a broad base with deep interdigitations in the basal plasma membrane; this membrane is closely associated with the basal lamina, which is exposed to the haemolymph. The smaller apical surface facing the digestive gland lumen carries microvilli. The cells contain spheres, which are composed of concentrically arranged layers inside a large membrane-bound vesicle. The layers consist of an organic matrix and magnesium phosphate salts; the latter are often dissolved and lost after fixation. In the opisthobranch *Cuthona granosa*, specimens 0.5 mm in length, just growing their first pair of cerata with digestive gland processes, exhibit similar granules. Their precursors seem to be formed in the Golgi complex (Schmekel & Wechsler, 1968a, b). Fretter (1939) depicted birefringent granules especially in *Scaphander* and *Haminea*. Most of these spherules are thought to contain calcium without having been tested.

A variety of functions has been proposed for the intracellular, mineralized concretions. In gastropods, the mineralized concretions exist as phosphate and carbonate types. The variation in composition reflects differences in function. The insoluble magnesium or calcium phosphate spheres occur in the digestive gland and under polluted conditions can sequester other metals, including manganese, cobalt, nickel, and zinc (Nott, 1991; Nott & Nicolaidou, 1989, 1990). This type is primarily concerned with detoxification of certain metals. The magnesium or calcium carbonate concretions occur in specialized cells of the connective tissue and are associated with shell regeneration and the regulation of pH and ionic balance of the body fluids (Simkiss, 1976; Taylor & Simkiss, 1984; Simkiss & Mason, 1984; Simkiss et al., 1982; Viarengo & Nott, 1993). The carbonate granules do not accumulate toxic cations (Mason & Nott, 1981). The exact function of the mineralized granules in the shell-less *Runcina* has yet to be investigated.

In *Lymnea* and many other mollusks, nephrocytes also

possess mineral-containing granules (Bonga & Boer, 1969). The histological appearance of the nephrocytes resembles the mineral-containing granule cells. Endodermal and mesodermal cell types seem to acquire similar structures to fulfill comparable functions.

ACKNOWLEDGMENTS

One of the authors (A.K.) wishes to thank the Director of the Marine Biological Association in Plymouth for kindly providing working facilities. The authors are grateful to H. Schaller, M. Bäschlin, and G. Morson for very skillful technical assistance and to D. Müller for secretarial help. We thank B. Peretti for the drawing and H. J. Stöcklin for the photographic preparations.

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Three New Species of *Bathymodiolus* (Bivalvia: Mytilidae) from Hydrothermal Vents in the Lau Basin and the North Fiji Basin, Western Pacific, and the Snake Pit Area, Mid-Atlantic Ridge

by

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Abstract. Three new species of *Bathymodiolus* are described and compared with *Bathymodiolus thermophilus* Kenk & Wilson, 1985: *B. brevior* from the Lau Basin and the North Fiji Basin, *B. elongatus* from the North Fiji Basin, and *B. puteoserpentis* from the Snake Pit area, Mid-Atlantic Ridge.

INTRODUCTION

The genus *Bathymodiolus* Kenk & Wilson, 1985, first collected in 1977 at hydrothermal vents on the Galapagos rift spreading zone (East Pacific Rise system) (Corliss & Ballard, 1977; Corliss et al., 1979), has been considered monotypic, its type species being *B. thermophilus* Kenk & Wilson, 1985. Since 1975, several expeditions to sites with hydrothermal vents or cold seeps in the Atlantic and Pacific oceans have taken place, and large mussels have been found in the benthic communities of many of the visited localities.

Bathymodiolus thermophilus was subsequently collected on a hydrothermal vent field of the East Pacific Rise, at 13°N, in a depth of 2630 m during the French-American expeditions BIOCYATHERM (March 1982), BIOCYARISE (March 1984), and HYDRONAUT (November 1987) (Desbruyères et al., 1982; Kenk & Wilson, 1985; Fustec et al., 1987; Tunnicliffe, 1991); however, other species were soon discovered at sites in the Atlantic and the western Pacific.

In the Atlantic, *Bathymodiolus*-like mytilids are now known from the Florida Escarpment, (26°2'N, 84°55'W,

3266 m), a cold sulfide and methane-enriched groundwater seep (Turner & Lutz, 1984; Paull et al., 1984; Hecker, 1985; Turner, 1985; fig. 4B–D; Gage & Tyler, 1991: fig. 15.13); from the continental slope off Louisiana, an area with hydrocarbon seeps (27°41'N, 91°32'W, 600–700 m and 27°47.5'N, 91°15.5'W, 640 m) (Childress et al., 1986; Kennicutt et al., 1988; MacDonald et al., 1990), from the Barbados Accretionary Prism, a cold seep region in a subduction zone (10°00'–10°35'N, 57°50'–59°00'W, 1000–2200 m) (Jollivet et al., 1990; Gage & Tyler, 1991; recent samples from the MANON and DIAPISUB expeditions); and from the Mid-Atlantic Ridge at 37°N (1500 m) (Gustafson, personal communication). The mussels of the mid-Atlantic Ridge site and the two Gulf of Mexico sites are now under study by R. Turner (Museum of Comparative Zoology, Harvard University, Cambridge), R. Gustafson and R. Lutz (Institute of Marine and Coastal Sciences, Rutgers University of New Jersey); and the species from the Barbados Accretionary Prism by R. von Cosel and B. Métivier (Muséum National d'Histoire Naturelle, Paris, France).

Another *Bathymodiolus*-like species was collected in June

1988 by the French submersible *Nautille* during the HYDROSNAKE expedition to the "Snake Pit" area, a hydrothermal vent region on a slow-spreading part of the Mid-Atlantic Ridge (23°23'N, 44°56'W, 3480 m) (Desbruyères, 1989; Tunncliffe, 1991; Segonzac, 1992:596; see also Mevel et al., 1989).

Most western Pacific hydrothermal sites were also found populated with mussels—the Okinawa Trough (Hessler & Lonsdale, 1991), the hydrothermal vents of the Mariana Trough at 3595–3666 m (Hessler & Lonsdale, 1991), and the Fiji and Lau Back Arc Basins (Desbruyères, 1989; Jollivet et al., 1989).

In 1989, numerous specimens of two species of large mussels were sampled by the submersible *Nautille* during the French BIOLAU cruise to the Lau Back Arc Basin and the joint French-Japanese STARMER II expedition to the Fiji Back Arc Basin. One of these species was found on all four explored sites: the "Vailili" hydrothermal vent field and the site "Hine Hina" (without smokers) on the Valufa ridge, Lau Basin, southeast of the Fiji Islands and the "White Lady" and "Mussel Valley" sites in the North Fiji Basin. The other species was encountered only on the latter two sites. In the North Fiji Basin, both species occur sympatrically. The German research vessel *Sonne* collected *Bathymodiolus*-like specimens in the Lau Back Arc Basin as well. However, from the hydrothermal fields on the Manus spreading center in the Manus Back Arc Basin (Bismarck Sea, Papua New Guinea), no hydrothermal vent mussels have yet been recorded (Tufar, 1990; Tufar & Jullmann, 1991).

In this paper, the two western Pacific species from the BIOLAU and STARMER expeditions and the Atlantic species from the HYDROSNAKE expedition are described and compared with *Bathymodiolus thermophilus*.

MATERIAL AND METHODS

Most of the studied material, as well as the reference material of *Bathymodiolus thermophilus*, was collected during the cruises BIOCYATHERM, BIOCYARISE, HYDRONAUT, HERO '92, HYDROSNAKE, BIOLAU, and STARMER II aboard the French research vessel *Nadir*, with the submersibles *Cyana* and *Nautille*, organized by IFREMER (Institut Français de Recherche pour l'Exploitation de la Mer). The collected material was sorted by the Centre National de Tri d'Océanographie Biologique (CENTOB), Brest. The material obtained by the R/V *Sonne* was borrowed from the Senckenberg Museum, Frankfurt. The measurements of length and height were taken according to Kenk & Wilson (1985:fig. 1). The bulk of the material is deposited in the Muséum National d'Histoire Naturelle, Paris, France; and material from the STARMER II expedition is also in the National Science Museum, Tokyo, Japan; paratypes were sent out to several major museums. The statistical analyses were carried out using STATVIEW 512 + TM.

Abbreviations used in the text: AMS—Australian Museum, Sydney, Australia; BMNH—British Museum (Natural History) (now: The Natural History Museum), London, U.K.; LACM—Los Angeles County Museum of Natural History, Los Angeles; MCZ—Museum of Comparative Zoology at Harvard University, Cambridge, Massachusetts; MNHN—Muséum National d'Histoire Naturelle, Paris, France; NMNZ—National Museum of New Zealand, Wellington, New Zealand; NSMT—National Science Museum, Tokyo, Japan; SMF—Natur-Museum und Forschungsinstitut Senckenberg, Frankfurt/M., Germany; USNM—National Museum of Natural History, Smithsonian Institution, Washington, D.C.; ZMB—Museum für Naturkunde (formerly: Zoologisches Museum) der Humboldt-Universität Berlin, Germany; spm.—specimen, specimens; sta.—sampling station.

SYSTEMATICS

Family MYTILIDAE

Subfamily BATHYMODIOLINAE Kenk & Wilson, 1985

Bathymodiolus brevior von Cosel, Métivier & Hashimoto, sp. nov.

(Figures 1–10, 26, 30–34, 37, 38)

Type material: Holotype, MNHN, BIOLAU expedition, Lau Basin, Vailili vent field: 4 paratypes, same locality, MNHN, dry shells; 4 paratypes, MNHN, as alcohol-preserved specimens; 4 other paratypes, 1 in NSMT, 1 in USNM, 1 in MCZ, 1 in SMF, all same locality, preserved in alcohol. Hine Hina hydrothermal field, BIOLAU expedition, dive BL 01, 22°32'S, 176°43'W, 1842 m, 13 May 1989, A. Dinet, observer: 23 paratypes, 8 in MNHN, 1 in NSMT, 1 in USNM, 2 in MCZ, 2 in LACM, 2 in AMS, 2 in NMNZ, 2 in BMNH, 1 in SMF, 2 in ZMB.

Type locality: Vailili vent field, Valufa Ridge, Lau Basin, 23°13'S, 176°38'W, 1750 m, BIOLAU, dive BL 12, P. Crassous, observer, 24 May 1989.

Description: Shell large, up to 140 mm long, rather thin but solid, modioliform-oval, somewhat variable in outline, inflated, equivalve, length/height ratio 1.6–2.2. Juvenile specimens shorter and more oval than adults (Figures 7, 10). Beaks subterminal, at one-seventh of total shell length. Anterior margin rather broadly rounded; ventral margin in juvenile, half-grown, and subadult specimens somewhat convex or straight; in large, fully grown specimens more or less concave. Postero-ventral margin broadly rounded, postero-dorsal margin slightly convex to almost straight; postero-dorsal corner narrowly rounded; ligament plate slightly arched. Exterior smooth, with well-developed, irregular growth lines, dull. Some specimens with very faint, broad radial undulations visible on postero-dorsal slope, bifurcating and thus somewhat reminiscent of the sculpture of *Brachidontes*. Umbo broad, somewhat flattened.

Shell without periostracum dull whitish; interior nacreous white.

Periostracum strong, dark brown, in umbonal region lighter brown, smooth, somewhat dull, with no periostracal hairs (however, byssal endplates of other specimens always scattered over valve).

Hinge without teeth, anterior hinge margin slightly protruding toward ventral. Ligament opisthodontic, strong, extending over whole postero-dorsal margin to postero-dorsal corner. Subligamental shell ridge faint from under umbos to middle of ligament, then becoming obsolete, under beaks visible only in ventral and not in lateral view (Figure 4). Anterior adductor scar long-oval, arched, situated in front of umbo. Posterior adductor scar rounded-trapezoid, united with posterior scar of posterior pedal and byssus retractor muscle. Anterior scar of same muscle separated and situated under ligament, at about two-thirds of its length (Figure 4). In juvenile specimens (up to 40–50 mm), scar located under end of ligament. Anterior byssus retractor muscle scar just under beak, on anterior part of umbonal cavity, visible only in posterior and ventral view but not in lateral view of interior. Pallial line ventrally only slightly concave or straight.

Larval shell 400 μ m long and nearly 400 μ m high. Separation present between very small protoconch I (about 100 μ m long) and large protoconch II, which indicates a long planktonic larval phase (Figures 30–33).

Animal with large ctenidia which are slightly more than two-thirds shell length; outer and inner demibranch of nearly equal size. Inner mantle folds separate along whole ventral margin length from anterior adductor to posterior margin. Mantle folds on anterior end pass from ventrally over anterior adductor muscle up- and forward along anterior margin, then fold down- and backward to pass again lower end of anterior adductor muscle toward ventral margin. Short, narrow, and rather strong and thick valvular siphonal membrane reaching from postero-ventral corner to siphonal opening, without papilla toward anterior margin (Figure 26, right). Foot thick, broad, and flattened, with ventral byssal groove two-thirds length of foot. Foot-byssus retractor muscle complex with anterior retractor moderately long; posterior byssus retractors consisting of two rather strong, diverging muscle bundles with common base at base of byssus. Anterior bundle short and broad, arising rather steeply toward attachment point on

shell interior; posterior bundle longer and equally thick or thinner, passing at very low angle to longitudinal shell axis toward attachment point directly in front of posterior adductor. Posterior foot retractor well developed, arising from base of foot, well in front of base of byssus retractor muscles, passing outer side of anterior retractor toward anterior bundle of posterior byssus retractor; reaching inner shell surface closely appressed to anterior bundle over half to two-thirds its length. Labial palps narrow-triangular, anterior two slightly smaller than posterior pair.

Selected measurements (length, height, tumidity) with length–height ratios:

143.5 × 65.0 × 56.1 mm paratype MNHN	BL 12	2.2
140.1 × 63.9 × 57.6 mm paratype MNHN	BL 12	2.2
133.5 × 62.2 × 56.7 mm paratype MNHN	BL 12	2.1
132.5 × 67.5 × 60.5 mm holotype	BL 12	2.0
127.9 × 63.0 × 55.0 mm paratype MNHN	BL 12	2.0
127.5 × 61.3 × 52.5 mm paratype MNHN	BL 12	2.1
125.6 × 61.7 × 50.6 mm paratype MCZ	BL 12	2.0
125.3 × 59.8 × 56.4 mm paratype MNHN	BL 12	2.1
124.7 × 57.8 × 53.6 mm paratype MNHN	BL 12	2.15
112.8 × 53.8 × 50.9 mm paratype NSMT	BL 12	2.1
108.5 × 51.3 × 42.1 mm paratype USNM	BL 12	2.1
104.3 × 50.2 × 40.8 mm paratype MNHN	BL 01	2.1
104.1 × 52.7 × 42.4 mm paratype SMF	BL 12	2.0
103.8 × 53.5 × 39.3 mm paratype MNHN	BL 01	1.9
103.3 × 53.1 × 42.3 mm paratype AMS	BL 01	1.9
103.2 × 48.4 × 40.0 mm paratype SMF	BL 01	2.1
102.3 × 51.0 × 41.3 mm paratype LACM	BL 01	2.0
102.1 × 50.8 × 41.1 mm paratype NSMT	BL 01	2.0
101.6 × 50.5 × 42.7 mm paratype MNHN	BL 12	2.0
98.3 × 51.4 × 40.0 mm paratype USNM	BL 01	1.9
98.0 × 49.8 × 37.5 mm paratype NMNZ	BL 01	2.0
96.4 × 47.7 × 39.4 mm paratype ZMB	BL 01	2.0
93.8 × 48.5 × 38.2 mm paratype LACM	BL 01	1.9
90.2 × 47.7 × 36.4 mm paratype MNHN	BL 01	1.9
89.1 × 45.0 × 38.9 mm paratype MNHN	BL 12	2.0
88.4 × 45.3 × 37.3 mm paratype NMNZ	BL 01	2.0
86.2 × 42.0 × 34.8 mm paratype BMNH	BL 01	2.1
84.7 × 44.3 × 33.1 mm paratype BMNH	BL 01	1.9
84.1 × 40.3 × 33.3 mm paratype MNHN	BL 01	2.1
83.8 × 44.0 × 32.2 mm paratype ZMB	BL 01	1.9
81.5 × 44.1 × 33.1 mm paratype MNHN	BL 01	1.8
81.5 × 39.0 × 30.7 mm paratype AMS	BL 01	2.1
78.7 × 44.0 × 31.4 mm paratype MNHN	BL 01	1.8
74.0 × 39.8 × 31.1 mm paratype MCZ	BL 01	1.9
66.0 × 35.0 × 24.1 mm paratype MCZ	BL 01	1.9
62.1 × 36.1 × 25.0 mm paratype MNHN	BL 01	1.7
48.8 × 30.2 × 20.3 mm paratype MNHN	BL 01	1.6

Explanation of Figures 1–5

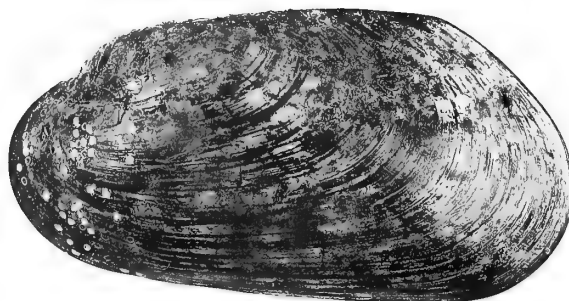
Figures 1–5. *Bathymodiolus brevior* von Cosel, Métivier & Hashimoto, sp. nov. Figure 1. Holotype, MNHN, 132.5 mm. Vailili vent field, Lau Basin, 23°13'S, 176°38'W, 1750 m, BIOLAU, dive BL 12. Exterior and interior of right valve, dorsal view, exterior of left valve. Figure 2. Exceptionally bean-shaped specimen, 86.9 mm., perhaps another species, BIOLAU, dive BL 05. Ventral view of the animal showing foot with byssus and the large gills, and exterior of right valve. Figure 3. Specimen from Mussel Valley, 111.9 mm, STARMER II, dive PL 19. Exterior of left valve (see also Figure 8). Figure 4. Paratype, MNHN, 140.0 mm, BIOLAU, dive BL 12. Interior of right valve. The muscle impressions in this and most following interior of valve views are marked with pencil. Figure 5. Paratype MNHN, 103.6 mm, dive BL 1. Interior and exterior of left valve and ventral view to show the position of foot/byssus retractor muscle scars.



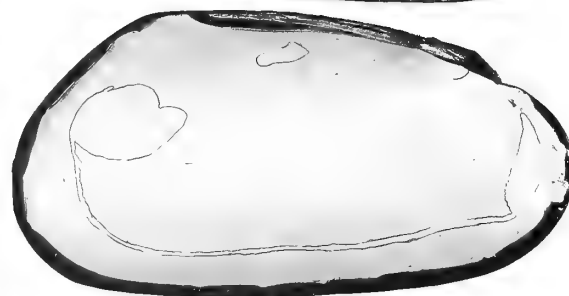
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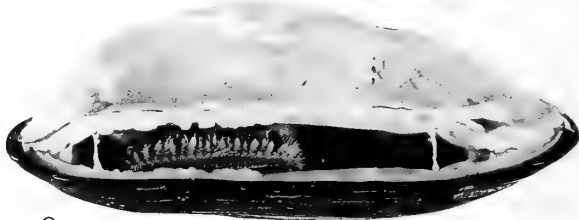
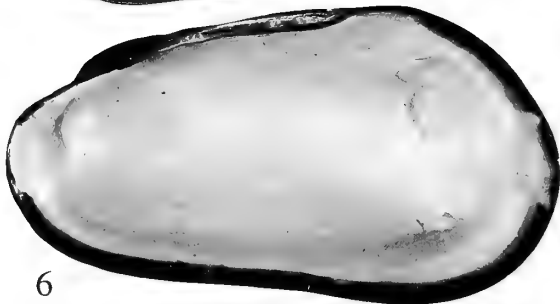
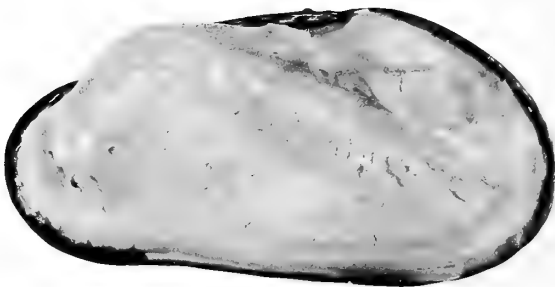
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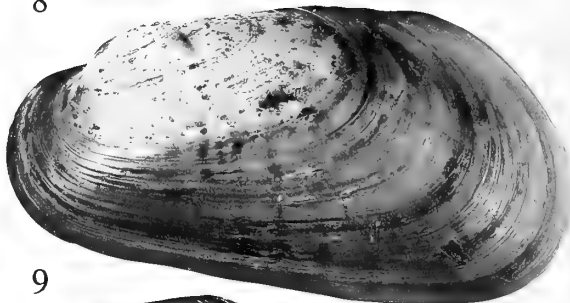


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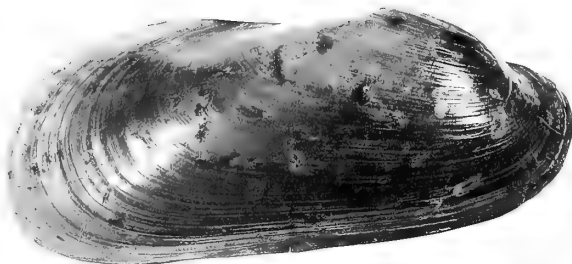
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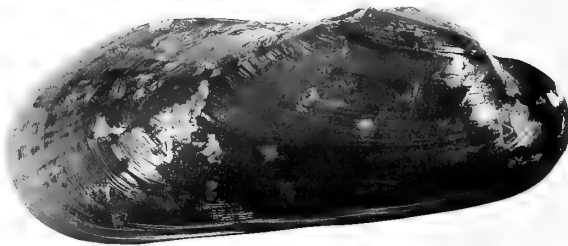
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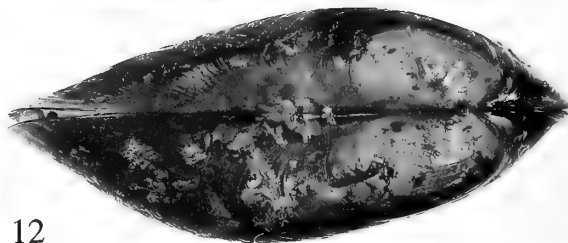
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Material examined: Type material; other material: Lau Basin, Vailili hydrothermal field (with smokers): BIOLAU dive BL 04, 23°13'S, 176°38'W, 1750 m, 16 May 1989, A. Dinét, observer, 12 spm.; BIOLAU dive BL 12, same locality, 24 May 1989, P. Crassous, observer, 3 spm. Hine Hina hydrothermal field (without smokers): BIOLAU dive BL 01, 22°32'S, 176°43'W, 1842 m, 13 May 1989, A. Dinét, observer, 40 spm.; BIOLAU dive BL 03, same locality, 1853 m, 15 May 1989, G. Barbier, observer, 106 spm.; BIOLAU dive BL 05, South of Hine Hina, 1885 m, 17 May 1989, A. Fiala, observer, 16 spm., all MNHN; 22°12,73'S, 176°36,43'W–22°13,06'S, 176°36,57'W, 1757–1703 m, dredged, R/V *Sonne*, cruise 67–2, sta. 183 GA, 26 spm., SMF. North Fiji Basin, White Lady hydrothermal field: STARMER II, dive PL 10, 16°59,5'S, 173°55,4'W, 2750 m, 5 spm.; STARMER II, dive PL 11, 16°59,5'S, 173°55,47'W, 2750 m, 5 spm.; STARMER II, dive PL 13, 16°59,5'S, 173°45,47'W, 2750 m, 4 spm.; STARMER II, dive PL 20, 16°59,5'S, 173°55,47'W, 2000 m, 24 spm.; Mussel Valley hydrothermal field: STARMER II, dive PL 19, 18°50'S, 173°29,0'W, 2750 m, 1 spm.

Habitat: The specimens live byssally attached to hard bottom around the hydrothermal vents; photos taken during the dives show dense clusters of mussels which are attached to each other in several layers. At the “White Lady” site, the mussels were grouped in a concentric ring around the vent where the water temperature was 3–4°C. Closer to the vent, the gastropods *Alviniconcha* (at temperatures of 10–20°C) and *Ifremeria* (at temperatures of 5–8°C) were found (Bouchet & Warén, 1991). The site is described in detail by Jollivet et al. (1989).

Distribution: Known from the North Fiji Basin and the Lau Basin, Fiji back arc.

Etymology: *brevior* (Latin) = shorter, referring to the difference in length/height ratio compared to the other mussel of the North Fiji Basin (see next description) and the working name “stout” given to this mussel.

Remarks: The major difference between *B. brevior* and *B. thermophilus* in the soft parts is the absence of fusion of the inner mantle folds along the anterior half of the ventral

margin. The “valvular siphonal membrane” (Kenk & Wilson, 1985) along the posterior part of the ventral margin (which also results from fusion of the inner mantle folds) in *B. thermophilus* reaches nearly to the middle of the shell. It ends in a central marginal papilla, leaving a very small byssal-pedal gape between it and the anterior mantle fusion, whereas in *B. brevior*, the membrane is stronger and terminates at the postero-ventral corner, without a papilla. In *B. brevior*, the posterior bundle of the posterior byssus retractor is somewhat thinner, and the angle of divergence of both bundles larger than in *B. thermophilus*. (compared with fig. 5 of Kenk & Wilson, 1985). In *B. brevior*, the anterior retractor attaches more anteriorly.

The shell of *B. brevior* is somewhat stouter and more tumid than that of *B. thermophilus*. It has a broader anterior part and a longer dorsal margin and ligament; the umbo is placed slightly more posteriorly. The scar of the anterior part of the posterior byssus retractor muscle is situated more forward and at a greater distance from the scar of the posterior part of the byssus retractor muscle, which is united with the posterior adductor scar. Moreover, in *B. thermophilus*, it is situated under the end of the ligament, but in adult *B. brevior* at two-thirds of the ligament length. The ligament of the new species ends abruptly just in front of the postero-dorsal corner, whereas in *B. thermophilus*, it ends in a more or less pronounced taper. The subligamental shell ridge, which in *B. thermophilus* is prominent under the beaks, is rather weak throughout the ligament length in *B. brevior* and becomes obsolete toward the ligament end. The anterior byssus retractor scar in *B. thermophilus* is situated in the umbonal cavity behind the beak; in *B. brevior*, it is directly under the beak. The ventral pallial line of *B. thermophilus* is markedly deflected upward in its anterior part, whereas in *B. brevior*, it is nearly straight. The color of the periostracum in *B. thermophilus* tends toward olive-brown, whereas in most observed specimens of *B. brevior*, it tends toward mahogany.

The adult specimens of *B. thermophilus* from the Galapagos Rift vents figured by Kenk & Wilson (1985:figs. 2–3) are more or less arcuate, whereas the 13 examined specimens of that species from the East Pacific Rise (13°N), (maximum length: 152 mm) have a straight to only weakly concave ventral margin; their byssal-pedal opening is

←

Explanation of Figures 6–12

Figures 6–10. *Bathymodiulus brevior* von Cosel, Métivier & Hashimoto, sp. nov. Figure 6. Juvenile specimen, 53.8 mm, BIOLAU, dive BL 03. Exterior and interior of right valve. Figure 7. Paratype MNHN, juvenile specimen, 78.8 mm, BIOLAU, dive BL 1. Exterior of left valve. A very short and high specimen. Figure 8. Specimen from Mussel Valley, 111.9 mm, STARMER II, dive PL 19. Ventral view, left valve removed. Note the polychaete worm in the pallial cavity (The two small sticks keep the mantle edges open) (see also Figures 3 and 26). Figure 9. Specimen with clear-colored periostracum, 89.8 mm, BIOLAU, dive BL 05. Exterior of left valve. Figure 10. Juvenile specimen, 34.5 mm, BIOLAU, dive BL 03. Exterior of left valve. Figures 11–12. *Bathymodiulus elongatus* von Cosel, Métivier & Hashimoto, sp. nov. Figure 11. Holotype, MNHN, 140.6 mm, “Mussel Valley” site, North Fiji Basin, 18°50'S, 173°29'W, 2765 m, STARMER II dive PL 18. Exterior and interior of right valve. Figure 12. Paratype, MNHN, 115.9 mm, Same locality. Exterior of right valve and dorsal view.

somewhat larger than in the Galapagos Rift specimens as figured by Kenk & Wilson (1985:fig. 8). There are reported genetic differences between the Galapagos Rift and the 13°N populations (Grassle, 1985); nevertheless, they are here considered conspecific. A strongly bean-shaped mussel was taken during the BL 05 dive (Figure 2); this is considered an aberrant specimen of *B. brevior*, but it might also represent another, still unnamed, species.

Bathymodiolus elongatus von Cosel, Métivier & Hashimoto, sp. nov.

(Figures 11–20, 25, 28, 35, 37, 38)

Type material: Holotype, MNHN, STARMER II expedition, “Mussel Valley” site; 17 paratypes, same locality, MNHN, preserved in alcohol; 18 other paratypes: 2 in NSMT, 2 in LACM, 2 in USNM, 2 in MCZ, 2 in AMS, 2 in NMNZ, 2 in BMNH, 2 in SMF, 2 in ZMB, all from same locality, preserved in alcohol.

Type locality: “Mussel Valley” site, North Fiji Basin, 18°50'S, 173°29'W, 2765 m, STARMER II, dive PL 18, Y. Nojiri, observer. 13 July 1989.

Description: Shell large, up to 155 mm long, very thin and on ventral margin somewhat “elastic,” quite fragile, elongate-modioliform, variable in outline and tumidity but generally very inflated, equivalve, length/height ratio 1.9–2.5. Juvenile specimens shorter and less tumid than adults. Beaks well subterminal, at one-fifth to one-sixth of total shell length. Anterior margin generally rather narrowly rounded, ventral margin straight, slightly convex, or, in fully grown specimens, occasionally somewhat concave in middle part. Posterior margin ventrally more or less broadly rounded, postero-dorsal margin behind ligament slightly to markedly convex; postero-dorsal corner narrowly rounded to indistinct. Ligament plate slightly arched to nearly straight. Exterior with well-developed, irregular growth lines and with tendency to somewhat irregular, narrow to rather broad concentric grooves and striae, mostly on ventral part of valves, often extending forward to

anterior part, occasionally smaller and quite regular in middle part (Figure 19). In fully grown specimens, faint, broad radial undulations frequently visible on postero-dorsal slope, bifurcating and somewhat reminiscent of the sculpture of *Brachidontes* (Figures 12, 16). Several specimens with 4–6 broad and very faint transverse waves in middle of shell which occasionally cause undulation of concentric striae and may be marked by darker color of periostracum (Figures 15, 18). Umbo broad and somewhat flattened.

Shell without periostracum dull whitish; interior nacreous.

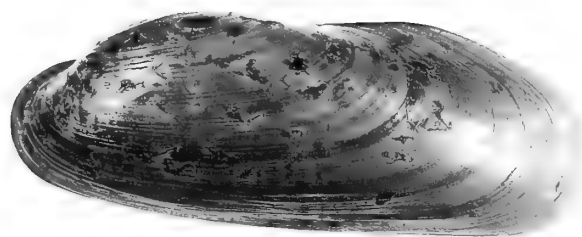
Periostracum strong, light chestnut brown, posterior umbonal region lighter brown, smooth, glossy, with no periostracal hairs but with byssal endplates of other specimens scattered over valve. Small, juvenile specimens with periostracum yellow.

Hinge without teeth, anterior hinge margin hardly protruding toward ventral. Ligament opisthodontic, moderately strong, extending to just in front of postero-dorsal corner. Subligamental shell ridge very faint from under umbos to middle of ligament, then becoming obsolete, under beaks visible only in ventral and not in lateral view (Figure 20). Anterior adductor scar broadly crescent-shaped, well in front of umbo. Posterior adductor scar rounded-trapezoid, united with posterior scar of posterior pedal and byssus retractor muscle. Anterior scar of same muscle separated, rather small and situated under ligament, at about two-thirds of it, in juvenile specimens (up to about 40–45 mm) located under end of ligament. Anterior byssus retractor scar in anterior part of umbonal cavity, just in front of beaks, visible only in posterior and ventral view but not in lateral view of interior. Pallial line only very weakly concave to straight.

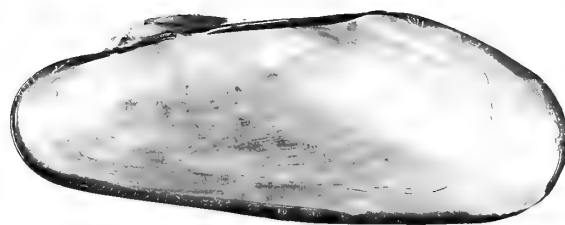
Animal with very large ctenidia which are slightly more than three-fourths of shell length; outer and inner demi-branch of nearly equal size (Figure 14). Mantle lobes separate from anterior end to postero-ventral extremity of shell margin. Mantle folds on anterior end passing ventrally over anterior adductor muscle fore- and upward along anterior margin for rather long distance, then folding

Explanation of Figures 13–20

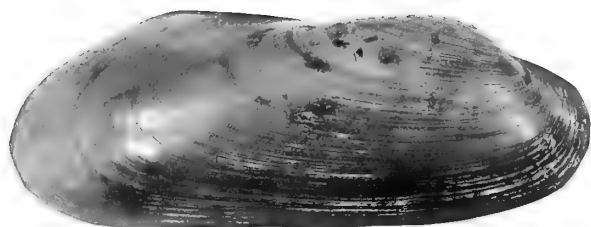
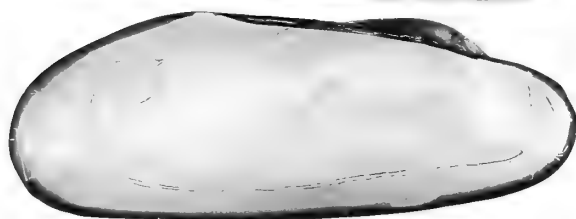
Figures 13–18. *Bathymodiolus elongatus* von Cosel, Métivier & Hashimoto, sp. nov. “Mussel Valley” site, STARMER II, dive PL 18. Figure 13. Paratype, LACM 2760, 125.8 mm. Exterior and interior of left valve. Strongly elongate specimen. Figure 14. Paratype, MNHN, 112.0 mm., Exterior of right valve and general view of preserved animal, right valve and mantle removed. Notice the large gills, the small foot and the small right labial palp just in front of the foot. Figure 15. Paratype, AMS C200706, 103.6 mm. Half-ventral view to show the undulations of the concentric striae in the middle near the ventral margin. Figure 16. Paratype, SMF 310427, 122.6 mm. Exterior of right valve. Note the shallow bifurcating radial undulations on the posterior part. Figure 17. Same specimen as on Figure 13. Interior and exterior of right valve. Figure 18. Paratype, MNHN, 95.1 mm. Exterior of left valve, showing black-marked transverse waves on the ventral part. Figure 19. *Bathymodiolus elongatus* von Cosel, Métivier & Hashimoto, sp. nov., STARMER II, dive PL 19, 96.3 mm. Exterior of left valve of a specimen showing quite regular concentric striae. Figure 20. *Bathymodiolus elongatus* von Cosel, Métivier & Hashimoto, sp. nov. Paratype, MNHN, STARMER II, dive PL 18, 131.5 mm. Interior of left valve and ventral view to show position of foot/byssus retractor muscle scars.



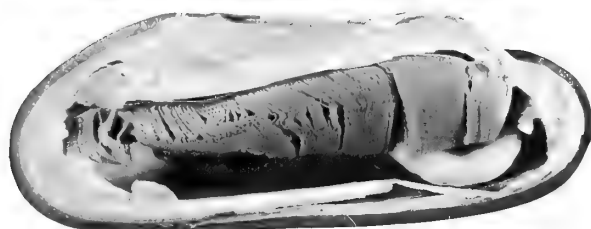
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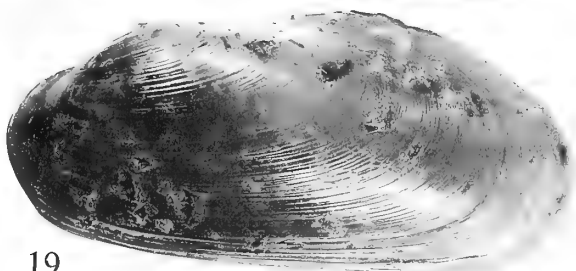
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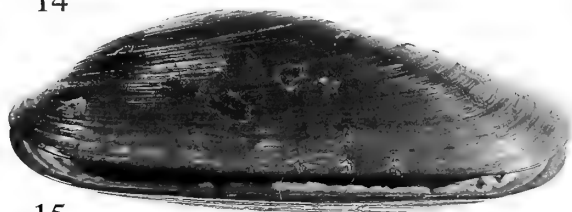
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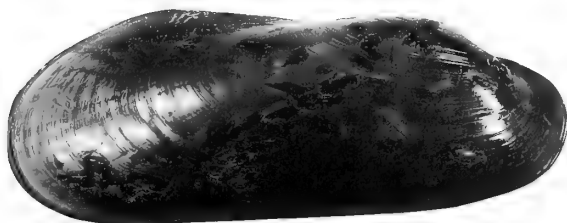
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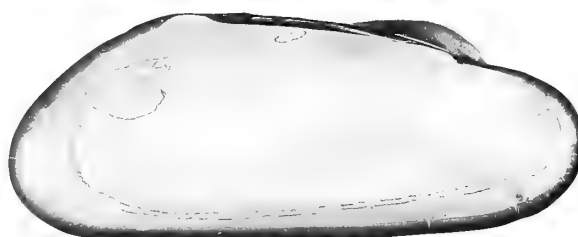
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down- and backward to again pass lower end of anterior adductor muscle toward ventral margin (Figure 25, left). Valvular siphonal membrane short and rather thin, reaching from postero-ventral corner to siphonal opening; no papilla present toward anterior margin (Figure 25, right). Foot thick, very broad and flattened, foot-byssus retractor muscle complex with rather short anterior retractor. Posterior byssus retractors consisting of two diverging muscle bundles with common base at base of byssus. Anterior bundle more or less short and broad and arising rather steeply toward attachment point on shell interior; posterior bundle long and thinner, passing at very low angle to longitudinal shell axis toward attachment point directly above and in front of posterior adductor. Posterior foot retractor well developed, arising from extreme anterior side of foot base, well in front of base of byssus retractor muscles, passing outer side of anterior retractor toward anterior bundle of posterior byssus retractor, reaching shell inside closely appressed to it over about half its length or more. Labial palps narrow-triangular, small but thick, anterior two slightly smaller than posterior pair.

Selected measurements (length, height, tumidity) with length-height ratios (all STARMER, sta. PL 18):

156.2 × 64.5 × 63.2 mm paratype MNHN	2.4
140.6 × 56.6 × 57.0 mm holotype	2.5
134.9 × 55.6 × 51.7 mm paratype MNHN	2.4
132.4 × 56.3 × 48.6 mm paratype MNHN	2.4
130.8 × 51.3 × 51.9 mm paratype MNHN	2.6
125.7 × 46.0 × 51.0 mm paratype LACM	2.7
122.6 × 47.0 × 46.7 mm paratype SMF	2.6
121.1 × 47.1 × 53.0 mm paratype NSMT	2.6
119.4 × 49.4 × 51.1 mm paratype USNM	2.4
113.6 × 42.0 × 46.0 mm paratype SMF	2.7
111.7 × 45.4 × 46.7 mm paratype LACM	2.5
111.2 × 43.6 × 44.8 mm paratype USNM	2.6
111.1 × 43.7 × 45.4 mm paratype MCZ	2.5
106.7 × 46.1 × 41.8 mm paratype AMS	2.3
105.6 × 41.5 × 43.8 mm paratype BMNH	2.5
103.8 × 42.6 × 42.2 mm paratype ZMB	2.4
103.5 × 44.6 × 37.0 mm paratype AMS	2.3
100.8 × 45.5 × 39.0 mm paratype NMNZ	2.2
99.8 × 41.8 × 37.8 mm paratype ZMB	2.4
95.5 × 38.8 × 35.7 mm paratype NSMT	2.4
95.1 × 37.7 × 35.3 mm paratype MCZ	2.5
94.5 × 39.1 × 38.5 mm paratype MCZ	2.4
90.6 × 40.4 × 36.2 mm paratype BMNH	2.3
85.5 × 37.2 × 33.2 mm paratype MNHN	2.3
69.5 × 32.5 × 26.9 mm paratype MNHN	2.1
57.7 × 28.8 × 21.3 mm paratype MNHN	2.0
52.2 × 26.6 × 18.3 mm paratype MNHN	2.0
41.2 × 23.1 × 15.1 mm paratype MNHN	1.8

Material examined: Type material; other material: North Fiji Basin, "Mussel Valley" site, 18°50'S, 173°29'W, 2765 m, STARMER II, dive PL 18, Y. Nojiri, observer. 13 July 1989, 106 spm.; STARMER II, dive 19, same locality and coordinates, 29 spm., all MNHN.

Habitat: The specimens were found byssally attached to lava around diffuse vents. The habitat is characterized by the absence of massive hydrothermal deposits and by low

temperature vent fluids not exceeding 8.5°C. The fluid venting was confirmed with the naked eye as "shimmering." Slender vestimentiferans, limpets (*Lepetodrilus elevatus*), bythograeid crabs (*Austinograea* cf. *williamsi*), and galatheids were found in the diffuse vent areas. For description of the site, see Jollivet et al. (1989).

Distribution: Known only from the North Fiji Basin.

Etymology: "Slender" (Latin: *elongatus*) was the working name for this mussel.

Remarks: No substantial differences were observed in the soft parts between *B. elongatus* and *B. brevior*. The valvular siphonal membrane seems thinner and slightly broader in the preserved specimens of *B. elongatus*, and the "back-folding" of the mantle lobes around the anterior adductor is more conspicuous (see Figure 25 vs. Figure 26). The configuration of the foot-byssus retractor complex is similar in both species; however, in *B. elongatus*, the anterior retractor is slightly shorter, and the posterior bundle of the posterior byssus retractor somewhat longer.

The shell of *B. elongatus* is easily distinguished from that of *B. brevior* by its markedly more slender, more elongate, and more tumid shape; the anterior end is narrower, and the beaks are situated still more backward. The length-height ratios of both species are plotted against shell length in Figure 37; they are substantially different in both species; and their change with size indicates allometric growth, which, however, is much more pronounced in *B. elongatus*.

For *B. brevior*, the graph shows a higher variability within the species, paired with a much less significant correlation between size and length-height ratio. The mean ratios are 1.95 for *B. brevior* and 2.30 for *B. elongatus* (see Table 3). The allometric growth of both species also causes the change of position with growth of the anterior portion of the posterior byssus-retractor scar from below the end of the ligament forward to below two-thirds of it.

The postero-dorsal margin behind the almost straight ligament plate is variable, from slightly to markedly convex, and, as a consequence, the postero-dorsal corner is narrowly rounded as in *B. brevior*, or indistinct. Moreover, *B. elongatus* has a much thinner and more fragile shell than *B. brevior*; the "elasticity" of the valves is demonstrated by the fact that on abrupt tight closing by the adductors, the ventral margin of one valve gives way to that of the other valve, and thus the ventral margins of the two valves appear slightly discordant. The anterior byssus retractor muscle scar is situated slightly more forward. The periostracum of *B. elongatus* is thinner and lighter colored than in most *B. brevior*. As in *B. brevior*, the ligament ends abruptly, but is somewhat shorter in relation to the total shell length.

Bathymodiolus thermophilus is less slender and more compressed with less prominent beaks; the beaks are situated more forward, the ligament is still shorter in relation to total shell length than in *B. elongatus*, and the scar of

Table 1
Comparison of some features in *Bathymodiolus*.

	<i>B. thermophilus</i> (from 13°N)	<i>B. brevior</i>	<i>B. elongatus</i>	<i>B. puteoserpentis</i>
General shell form	moderately elongate	somewhat stout	elongate	somewhat stout
Tumidity	more or less compressed	tumid	very tumid	moderately tumid
Shell	thin but solid	thin but solid	very thin and more fragile	thin but solid
Position of anterior part of posterior byssus retractor muscle scar	under the end of the ligament	at $\frac{2}{3}$ of the ligament	at $\frac{2}{3}$ of the ligament	under posterior third of ligament, near the end
Position of anterior byssus retractor scar in the umbonal cavity	slightly behind the beak	under and in front of the beak	under and in front of the beak	under and in front of the beak
Ventral pallial line	markedly deflected	nearly straight	straight	nearly straight
Mantle lobes on anterior half of ventral side	fused	separate	separate	separate
Valvular siphonal membrane	long and thin	short, narrow, rather strong	short	short
Posterior end of ligament	tapering	abrupt	abrupt	abrupt to slightly tapering
Subligamental shell ridge	strong and angular	faint from umbo to ligament middle, then obsolete	very faint from umbo to ligament middle, then obsolete	faint to obsolete, occasionally more marked

Table 2
Bathymodiolus brevior, length/height ratios from different localities.

	Ratio	Mean	SD	SE	<i>n</i>	Length (mm)	Mean
Regions							
N-Fiji Basin	1.7–2.2	1.945	0.115	0.018	39	40.4–137.2	92.6
Lau Basin	1.6–2.2	1.951	0.103	0.007	214	33.2–143.5	83.8
Hydrothermal fields							
Vailili	1.7–2.2	1.955	0.148	0.028	29	33.2–143.5	94.2
Hine Hina	1.6–2.2	1.950	0.094	0.007	185	45.5–111.1	82.1
White Lady	1.7–2.2	1.940	0.117	0.019	38	40.4–137.2	92.1
Mussel Valley	2.0	2.0	—	—	1	111.7	
Stations (dives)							
Hine Hina BL 01	1.6–2.2	1.945	0.110	0.014	63	45.5–104.2	84.2
Hine Hina BL 03	1.7–2.2	1.942	0.083	0.008	106	48.1–104.6	79.9
Hine Hina BL 05	1.9–2.2	2.020	0.069	0.017	16	65.7–111.1	88.6
Vailili BL 04	1.7–1.9	1.832	0.082	0.024	12	33.2–81.1	69.9
Vailili BL 12	1.8–2.2	2.042	0.120	0.029	17	49.6–143.5	111.4
White Lady PL 10	1.9–2.1	1.926	0.079	0.036	5	100.0–112.5	107.7
White Lady PL 11	1.9–2.2	2.008	0.113	0.051	5	90.0–137.2	110.5
White Lady PL 13	1.7–1.9	1.821	0.059	0.030	4	64.2–110.0	81.1
White Lady PL 20	1.7–2.2	1.955	0.120	0.025	24	40.4–129.3	86.8
Mussel Valley PL 19	2.0	—	—	—	1	111.7	
<i>B. brevior</i> "Sonne"	1.5–2.2	1.837	0.161	0.032	25	17.2–123.3	63.3

Table 3

Comparisons of length/height ratios of *Bathymodiolus brevior* and *Bathymodiolus elongatus*.

	Length/height ratio		SD	SE	n
	Ratio	Mean			
<i>B. brevior</i> total	1.6–2.2	1.950	0.105	0.007	253
<i>B. elongatus</i> total	1.8–2.8	2.297	0.179	0.015	149
<i>B. brevior</i> 90 mm and larger	1.8–2.2	2.010	0.084	0.009	90
<i>B. elongatus</i> 90 mm and larger	2.2–2.8	2.397	0.115	0.012	93
<i>B. brevior</i> smaller than 90 mm	1.6–2.2	1.914	0.099	0.008	158
<i>B. elongatus</i> smaller than 90 mm	1.8–2.4	2.123	0.136	0.019	53
<i>B. brevior</i> 60 mm and smaller	1.6–2.0	1.830	0.147	0.042	12
<i>B. elongatus</i> 60 mm and smaller	1.8–2.2	1.994	0.114	0.028	17
<i>B. brevior</i> 50 mm and smaller	1.6–2.0	1.757	0.143	0.054	7
<i>B. elongatus</i> 50 mm and smaller	1.8–2.0	1.880	0.007	0.029	6

Comparison (* = significant at 95%)

	Mean diff.	Fisher PLSD	Scheffe F-test
<i>B. elongatus</i> vs. <i>B. brevior</i> total	0.347	0.028*	602.297*
<i>B. elongatus</i> vs. <i>B. brevior</i> 90 mm and larger	0.386	0.029*	673.987*
<i>B. elongatus</i> vs. <i>B. brevior</i> smaller than 90 mm	0.209	0.034*	144.212*
<i>B. elongatus</i> vs. <i>B. brevior</i> 60 mm and smaller	0.163	0.099*	11.341*
<i>B. elongatus</i> vs. <i>B. brevior</i> 50 mm and smaller	0.123	0.142	3.611

the anterior part of the posterior byssus retractor is situated under the posterior end of the ligament. As in most *B. brevior* specimens, the periostracum of *B. elongatus* tends more toward a chestnut color than to the olive coloration observed in many specimens of *B. thermophilus*.

Although the differences in length/height ratio and coloration between *B. elongatus* and *B. brevior* are rather constant, there are specimens of *B. brevior* which seem to have a slightly tendency toward intergradation to *B. elongatus*, especially specimens from dive BL 05 at Hine Hina (BIOLAU cruise). These have a clear brown periostracum like *B. elongatus* and a slightly higher mean length/height ratio (2.02) than the "average" *B. brevior* (1.95, see Table 2) which, however, is still much lower than that of *B. elongatus* (2.18).

A one-way analysis of variance (ANOVA) including all available specimens was run to test the significance of the differences between *B. brevior* and *B. elongatus* in length/

height ratio ($F = 602.297$; $df = 1, 400$, $P < 0.001$) and length/tumidity ratio ($F = 50.533$; $df = 1, 398$, $P < 0.001$). In both parameters, the difference is significant at 95%.

1/h ratio:	mean difference:	0.347
	Fisher PLSD:	0.028*
	Scheffe F-test:	602.297*

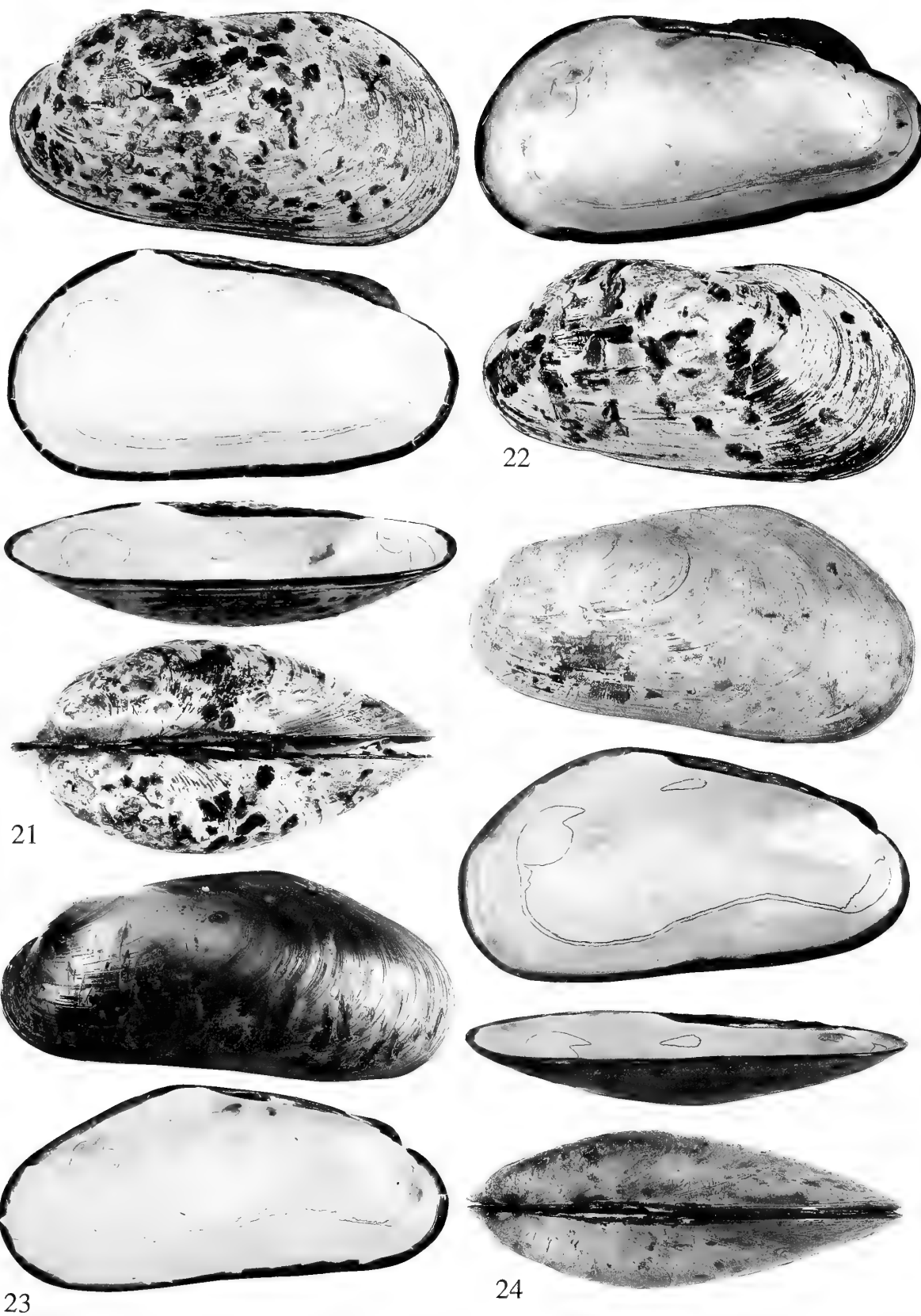
1/tumidity ratio:	mean difference:	0.125
	Fisher PLSD:	0.035*
	Scheffe F-test:	50.533*

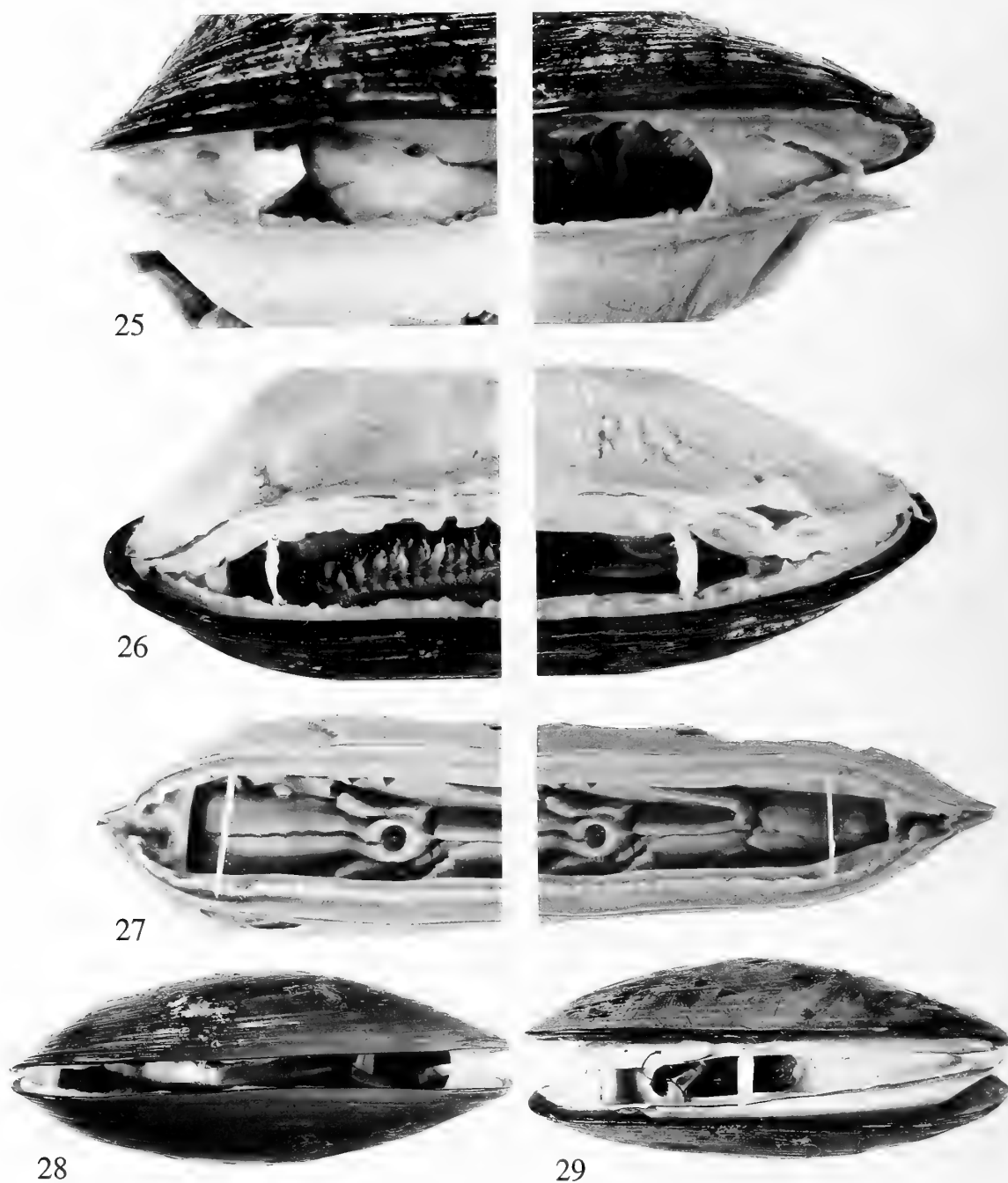
Separate calculations for the length-height ratio of *B. brevior* from the different localities showed only very slight and mostly non-significant differences.

* Significant at 95%.

Explanation of Figures 21–24

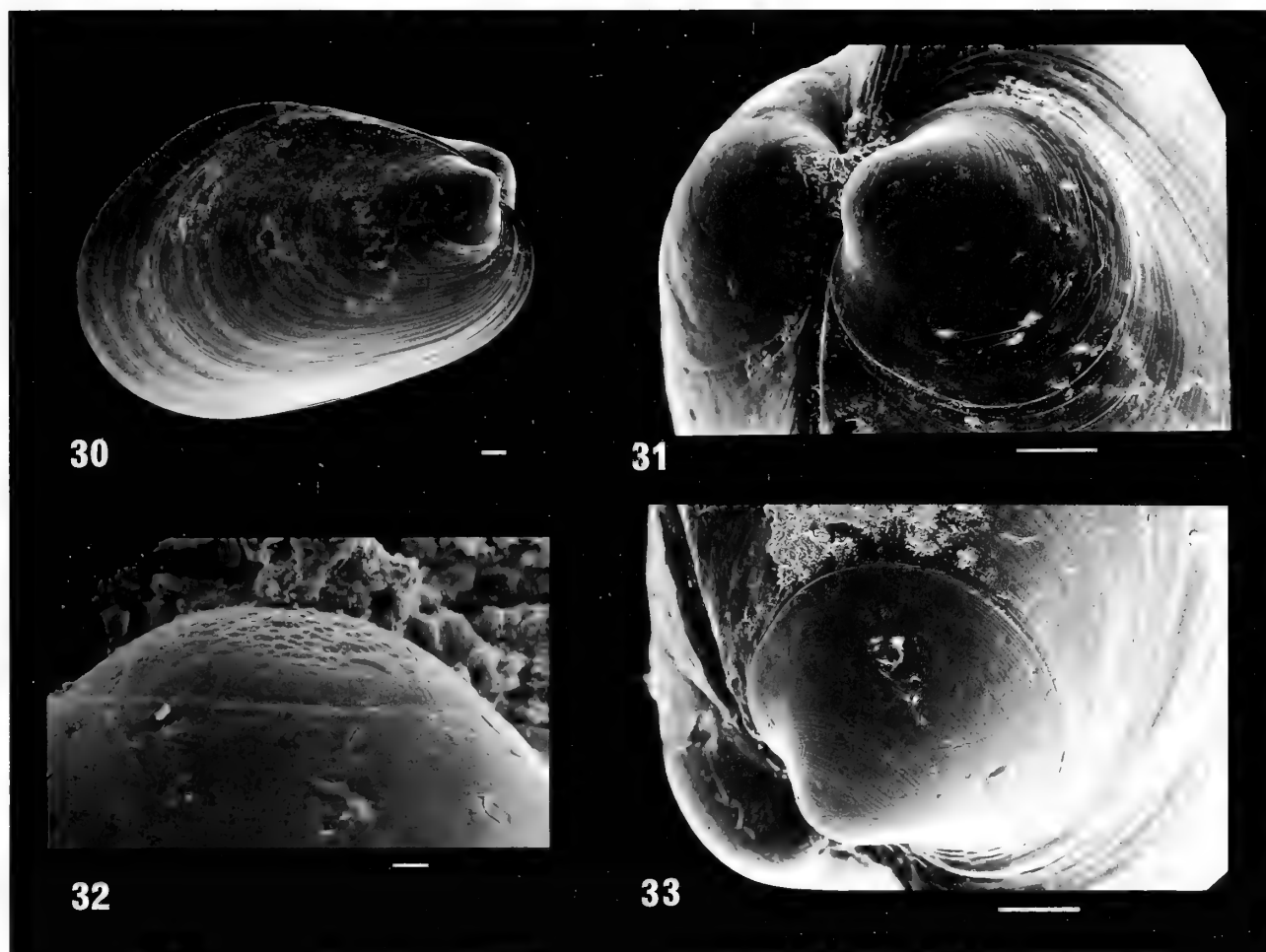
Figures 21–22. *Bathymodiolus puteoserpentis* von Cosel, Métiévier & Hashimoto, sp. nov. "L'Elan" site, Snake Pit hydrothermal field, Mid-Atlantic Ridge, 23°22'N, 47°57'W, 3515 m, HYDROSLAKE, dive HS 03. Figure 21. Holotype, MNHN, 112.3 mm. Exterior and interior of left valve, ventral view of left valve to show position of foot/byssus retractor muscle scars, dorsal view to show tumidity. Figure 22. Paratype, MNHN, 94.5 mm. Interior and exterior of left valve. Figures 23–24. *Bathymodiolus thermophilus* Kenk & Wilson. East Pacific Rise (13°N). Figure 23. 152.0 mm, BIOCYARISE '84, PL 45. Exterior and interior of left valve. Figure 24. 104.7 mm, HERO '92, dive 2523, Site "Genesis." Interior and exterior of left valve, ventral view of left valve to show position of foot/byssus retractor muscle scars (note the prominent subligamental shell ridge); dorsal view.





Explanation of Figures 25–29

Figure 25. *Bathymodiolus elongatus* von Cosel, Métivier & Hashimoto, sp. nov. Holotype. Close-up view of anterior and posterior mantle fusion and posterior valvular siphonal membrane. The anterior fusion is "turning back" above the anterior adductor. The posterior fusion is at the posterior end, posterior to the valvular membrane. Figure 26. *Bathymodiolus brevior*, von Cosel, Métivier & Hashimoto, sp. nov. Specimen from "Mussel Valley." Close-up view of anterior and posterior mantle fusion and posterior valvular siphonal membrane (the sticks keep the mantle openings open). Figure 27. *Bathymodiolus puteoserpentis* von Cosel, Métivier & Hashimoto, sp. nov. Close-up view of anterior and posterior mantle fusion and posterior valvular siphonal membrane (the sticks keep the mantle openings open). Figure 28. *Bathymodiolus elongatus* von Cosel, Métivier & Hashimoto, sp. nov. Paratype, SMF 310427 (see also Figure 16). Ventral view. Figure 29. *Bathymodiolus thermophilus* Kenk & Wilson. East Pacific Rise (13°N), HERO '92, Sta. 2523. Same specimen as on Figure 24. Ventral view. Comparison of both species to show extension of ventral opening.



Explanation of Figures 30–33

Figures 30–33. *Bathymodiolus brevior* von Cosel, Métivier & Hashimoto, sp. nov. BIOLAU, dive BL 03. SEM micrographs of embryonic and postembryonic shells. Figure 30. Juvenile specimen. Scale bar: 100 μ m. Figure 31. Protoconch I and II of the same specimen. Scale bar: 100 μ m. Figure 32. Close-up view of protoconch I. Scale bar: 10 μ m. Figure 33. Protoconch II of another specimen of the same lot. Scale bar: 100 μ m.

Bathymodiolus puteoserpentis von Cosel, Métivier & Hashimoto sp. nov.

(Figures 21–22, 27, 36, 38)

Bathymodiolus n. sp., Tunnicliffe, 1991:349

Type material: Holotype, MNHN, HYDROSNAKE expedition, Snake Pit hydrothermal field, Mid-Atlantic Ridge; 2 paratypes with preserved animal, same locality, in MNHN, 1 in MCZ; 5 paratypes, same locality, empty shells but live-collected: 1 in MNHN, 1 in NSMT, 1 in USNM, 1 in LACM, 1 in SMF.

Type locality: “L’Elan” (The Moose) site, Snake Pit hydrothermal field, Mid-Atlantic Ridge, 23°22’N,

47°57’W, 3515 m, HYDROSNAKE dive HS 03, J. Karson, observer, 21 June 1988.

Description: Shell rather large, up to 119 mm long, quite thin but solid, oval-modioliform, variable in outline and tumidity, equivalve, length/height ratio 1.8–2.0. Juvenile specimens more oval and more compressed than adults. Beaks subterminal, at one-seventh of total shell length. Anterior margin broadly to rather narrowly rounded, ventral margin straight or very weakly convex, in middle section or just before middle often somewhat concave. Postero-ventral margin broadly rounded, continuing to markedly convex postero-dorsal margin and more or less broadly rounded postero-dorsal corner. Ligament plate slightly arched in anterior part, tending toward straight in pos-

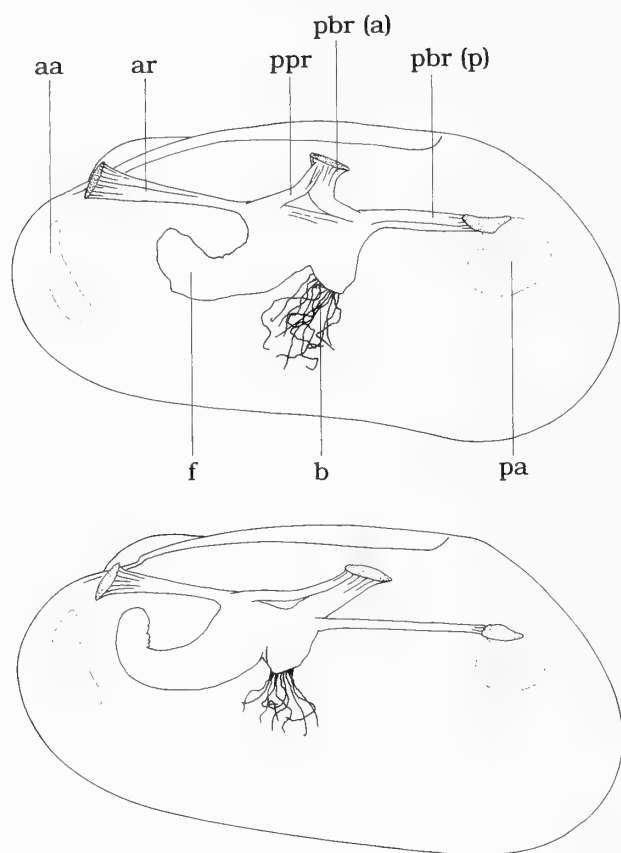


Figure 34

Sketch of foot-byssus retractor muscle complex of *Bathymodiolus brevior* von Cosel, Métivier & Hashimoto, sp. nov. and its position in the shell (separate slender strand of anterior retractor muscle serving as support for labial palps not drawn; ligament's position only marked). Above, specimen from BIOLAU BL 12, 89.1 mm, paratype MNHN; below, specimen from BIOLAU sta. BL 1, 90.2 mm (the different lengths of the corresponding muscle bundles in both specimens seem to be due to different degree of contraction in the moment of preservation). aa, position of anterior adductor; ar, anterior retractor muscle; ppr, posterior pedal retractor; pbr (a), posterior byssus retractor, anterior bundle; pbr (p), posterior byssus retractor, posterior bundle; f, foot; b, byssus; pa, position of posterior adductor.

terior part. Exterior smooth, with pronounced irregular growth lines. Umbo broad, somewhat flattened.

Periostracum strong, dark brown, and rather glossy. Valves irregularly covered with byssal endplates of other specimens, which in dried shells peel off.

Interior of valves white and nacreous.

Hinge without teeth but anterior hinge margin slightly protruding toward ventral. Ligament opisthodontic, strong, extending over most of postero-dorsal margin, leaving free very short part just in front of postero-dorsal corner. Subligamental shell ridge usually faint to obsolete; in some specimens, however, quite well marked. Anterior adductor

scar rather broad and nearly half-moon-shaped, situated in front of umbo. Posterior adductor scar large, united with posterior scar of posterior pedal and byssus retractor muscle; anterior scar of muscle separated and situated under posterior third of ligament or nearly under ligament's end. Anterior byssus retractor muscle scar in anterior part of umbonal cavity, just under beak, in extreme lower part occasionally visible in lateral view of interior of valve. Pallial line rather close to margin and nearly parallel to it.

Animal with very large ctenidia which are more than three-fourths of shell length; outer and inner demibranch of nearly equal size. Mantle lobes separate from anterior end to posterior shell margin, valvular siphonal membrane beginning at postero-ventral extremity of shell margin (a photo cannot be shown because in all available specimens, the adductors had been cut on board before preservation to allow quick entry of the preservation liquid via the open valves). Foot not very thick, flattened, tapering toward end and terminating in rather narrow tip, with ventral byssal groove three-fourths of foot length. Foot-byssus retractor muscle complex with moderately long anterior retractor. Posterior byssus retractors consisting of two strong, diverging muscle bundles with common base at base of byssus. Anterior bundle broad and arising steeply toward attachment point on shell inside. Posterior bundle long, rather strong, divided into two parallel bundles at about half its length (in observed specimen), passing at low angle to longitudinal shell axis toward attachment point directly in front and above posterior adductor. Posterior foot retractor broad, arising from base of foot, well in front of base of byssus retractor muscles, passing outer side of anterior retractor toward anterior bundle of posterior byssus retractor and reaching shell inside closely appressed to it, touching it at half to two-thirds its length. Labial palps triangular, small but thick, anterior two slightly smaller than posterior pair.

Measurements (length, height, tumidity) with length-height ratios:

112.2 × 56.3 × 51.2 holotype	HS 03	2.0
94.4 × 46.2 × 45.5 paratype MNHN	HS 03	2.0
85.2 × 48.4 × 39.0 paratype SMF	HS 03	1.8
82.6 × 45.0 × 37.3 paratype MNHN	HS 03	1.8
81.1 × 40.0 × 31.5	HS 10	2.0
80.4 × 45.6 × 38.1 paratype NSMT	HS 03	1.8
80.2 × 39.4 × 31.4	HS 10	2.0
76.1 × 40.2 × 32.5	HS 10	1.9
71.7 × 36.1 × 27.3	HS 10	2.0
71.3 × 38.5 × 34.2 paratype LACM	HS 03	1.9
68.0 × 34.5 × 28.3	HS 10	2.0
65.6 × 34.2 × 27.0	HS 10	1.9
60.4 × 37.2 × 31.2 paratype MCZ	HS 03	1.6
57.0 × 31.7 × 25.4 paratype USNM	HS 03	1.8

Material examined: Type material; other material: "Les Ruches" site, Snake Pit area, Mid-Atlantic Ridge, HYDRO-SNAKE expedition, dive HS 10, same coordinates, 3478 m, M. Segonzac, observer, 29 June 1988, 6 spm.,

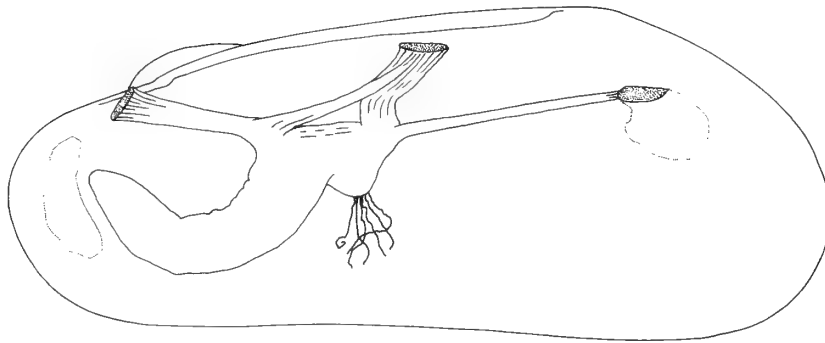


Figure 35

Sketch of foot-byssus retractor muscle complex of *Bathymodiolus elongatus* von Cosel, Métivier & Hashimoto, sp. nov. and its position in the shell. Specimen from STARMER sta. PL 19, 98.7 mm. For explanations, see previous figure.

MNHN (of a total of 23 specimens collected, 14 were available for this study).

Habitat: Byssally attached to sulphur blocks immediately around diffuse venting of water (Desbruyères, 1989; Segonzac, 1992).

Distribution: Known only from the Snake Pit area, Mid-Atlantic Ridge. The site is described by Mevel et al. (1989).

Etymology: The species is named after the site: *puteus* (Latin) = pit; *serpens* (Latin) = snake.

Remarks: The foot-byssus retractor complex of *B. puteoserpentis* (Figure 36) more closely resembles that of *B. thermophilus* (as figured in Kenk & Wilson (1985)) than those of *B. brevior* and *B. elongatus*; the anterior bundle of the posterior byssus retractor is longer; the posterior

bundle is stronger. The other observed anatomical characters are as in *B. brevior* and *B. elongatus*.

The shell of *B. puteoserpentis* in some aspects resembles that of *B. thermophilus*, but it is shorter and somewhat broader, a bit more inflated with a longer ligament in relation to shell length, a more forward-situated anterior byssus/foot retractor muscle scar, and chestnut-brown rather than olive-brown periostracum (as in the few examined *B. thermophilus*). *Bathymodiolus thermophilus* and *B. puteoserpentis* both have the anterior part of the byssus retractor scar located nearly below the end of the ligament and not at two-thirds the length of the ligament as in *B. brevior* and *B. elongatus*. There seems to be only a slight change of position with growth, judging from the smallest specimen seen (57 mm). The shell outline of *B. puteoserpentis* is roughly similar to that of *B. brevior*, but the Atlantic species seems to be more variable. The length/

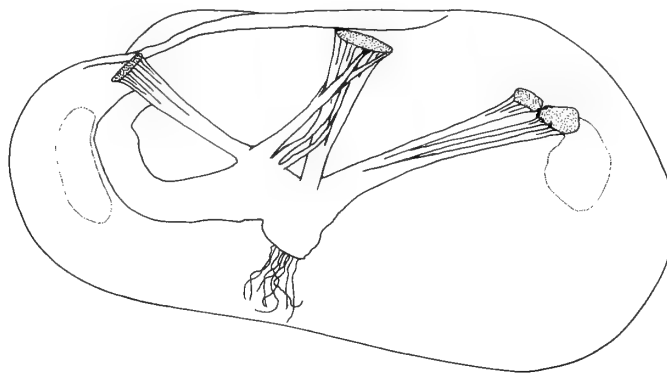


Figure 36

Sketch of foot-byssus retractor muscle complex of *Bathymodiolus puteoserpentis* von Cosel, Métivier & Hashimoto, sp. nov. and its position in the shell. Specimen from HYDROSLAKE sta. HS 03, 82.6 mm, paratype MNHN. For explanations, see Figure 34.

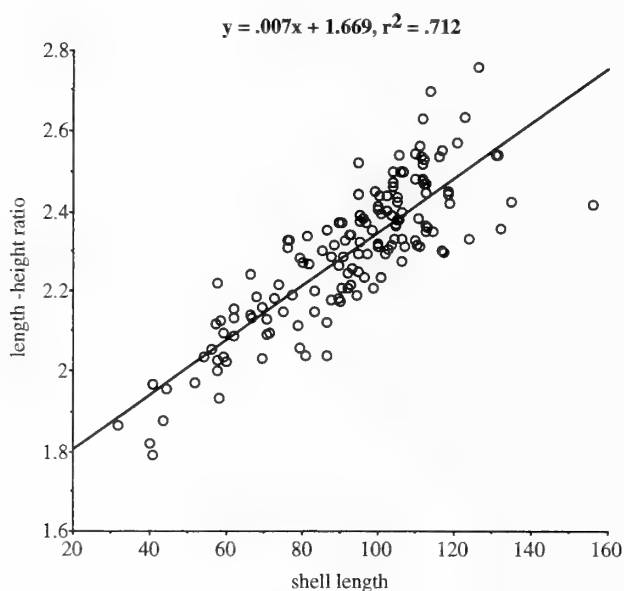
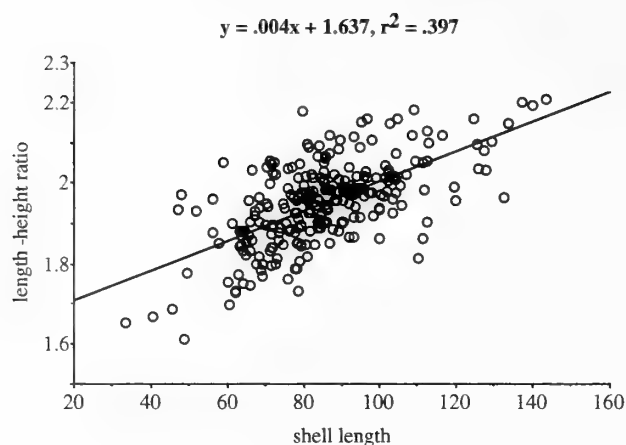


Figure 37

Length-height ratio vs. shell length in mm of *Bathymodiolus brevior* von Cosel, Métivier & Hashimoto, sp. nov. (all stations, $n = 253$) and *B. elongatus* (all stations, $n = 49$).

height ratio coincides with that of *B. brevior*, but is significantly different from that of *B. elongatus* (Figure 38).

DISCUSSION

The separation of *B. brevior*, *B. elongatus*, and *B. puteoserpentis* is based mainly on shell characters. The differences in shell shape between *B. brevior* and *B. elongatus* are quite evident in half-grown and adult specimens, but less evident in juvenile specimens. In very young specimens (under 50 mm), the differences are no longer significant (Table 3). In spite of the very close relationship, the differences in shell shape and thickness, as well as the sympatric occurrence of *B. brevior* and *B. elongatus* on one diving station (Mussel Valley, PL 19), leads us to

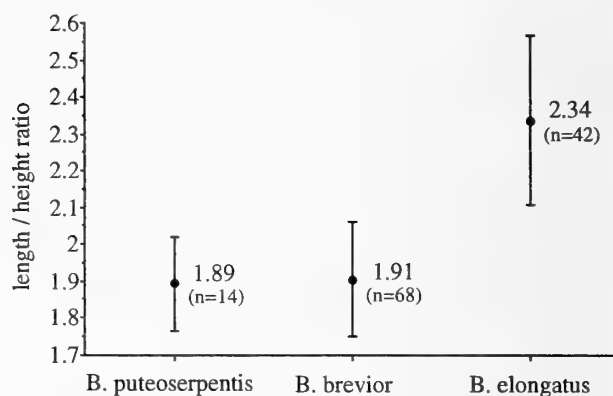


Figure 38

Length-height ratios of *Bathymodiolus elongatus*, von Cosel, Métivier & Hashimoto, sp. nov. *B. brevior* von Cosel, Métivier & Hashimoto, sp. nov. and *B. puteoserpentis* von Cosel, Métivier & Hashimoto, sp. nov. (Bars are 1 SD).

identify two different species although there seems to be a very slight tendency to intergrade.

The larval shell of *B. brevior* has a small protoconch I (100 μ m in length) and a large protoconch II (400 μ m in length), similar to *B. thermophilus* (Lutz et al., 1980).

The main differences between the three species here described and *B. thermophilus* are the fusion of the inner mantle folds along the anterior half of the ventral margin as well as a long valvular siphonal membrane in *B. thermophilus* (Figure 29) and the absence of this fusion and a short valvular siphonal membrane in the three new species (Figures 25–28). The foot-byssus retractor muscle complex exhibits the same basic configuration in all four species; however, in *B. thermophilus*, the anterior retractor attaches in the posterior part of the umbonal cavity, whereas in the three new species, it attaches on its anterior wall. The other differences between the retractor complexes are less conspicuous and concern the relative length and thickness of the different muscle bundles: in *B. brevior* and *B. elongatus*, the anterior bundle of the posterior byssus retractor tends to be shorter; it attaches more anteriorly in adult specimens; the posterior bundle tends to be thinner; the bundles are also more widely divergent than in *B. puteoserpentis* and *B. thermophilus*.

The assignment of the new species to *Bathymodiolus* is provisional. Of the possible genera *Adipicola* Dautzenberg, 1927 *Idasola* Iredale, 1915 (= *Idas* Jeffreys, 1876, non Mulsant, 1876; see Dell, 1987), *Benthomodiolus* Dell, 1987, and *Bathymodiolus*, the latter seems at the moment to be the most appropriate genus. *Adipicola* has an entirely different byssus retractor muscle system with no separate foot retractor (see Dell, 1987:fig. 42). In *Idasola*, the hinge line has typical, close-set vertical grooves, and the shell has periostracal bristles. Both characters are absent in our hydrothermal vent mussels; also the foot-byssus retractor muscle complex is different, and the posterior pedal re-

tractor and posterior byssal retractor are together in one (or two) bundles (see Dell, 1987:fig. 38–43). Apart from the size, the shells of *Benthomodiolus* are rather similar in shape to the new species, and also the foot-byssus retractor complex has the same general arrangement, although the posterior foot retractor is thinner in the two known *Benthomodiolus* (Dell, 1987, figs. 51, 52) than in our species. However, the presence of periostracal hairs in *Benthomodiolus* and their absence in *Bathymodiolus thermophilus*, as well as in the new species, is a reason for rejecting *Benthomodiolus* and placing our species for the moment in *Bathymodiolus*.

The presence or absence of the inner mantle fold fusion and differences in the valvular siphonal membrane are evidence for ultimately separating the new species from *Bathymodiolus* and establishing a new genus; however, a new genus should be erected only after a more thorough study of the internal anatomy of the new species (study currently under way by M. Le Pennec and A. Fiala) as well as study of the other deep-water mytilid genera.

The above mentioned differences between the eastern Pacific and western Pacific populations of hydrothermal vent mussels, as well as the differences in shell shape and positions of the adductor and foot-byssus retractor muscles, lead to the conclusion that the hypothesis of successive colonization of the western Pacific localities from sites in the eastern Pacific (or vice versa) by the planktonic larvae can be excluded. *Bathymodiolus thermophilus* is much more distinct from the western Pacific species than those are from each other.

The Atlantic *B. puteoserpentis* (and also the material from Barbados currently under study) has much closer affinity to the two western Pacific species than to *B. thermophilus*. If we assume that the inner mantle fold fusion is an apomorphic character and the absence of this fusion is plesiomorphic, it could be presumed that after the closure of the Isthmus of Panama, the eastern Pacific populations developed divergently from the remaining populations on the other side of the Isthmus, which remained more stable, as did the western Pacific populations.

ACKNOWLEDGMENTS

We would like to thank A.-M. Alayse, D. Desbruyères, S. Ohta, and the participants of the BIOLAU, STAR-MER, and HYDROSLAKE expeditions as well as M. Segonzac (CENTOB, French National Sorting Center, IFREMER Brest) for placing the collected material at our disposition. S. Gofas and two anonymous referees are thanked for reading the manuscript critically and proposing improvements. The assistance of D. Guillaumin (CIME, Dept. MEB, Université Paris-VI) for the SEM photos is gratefully acknowledged. For the loan of the material obtained by the R/V *Sonne*, we are indebted to R. Janssen (SMF).

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The Early Life History of *Bembicium vittatum* Philippi, 1846 (Gastropoda: Littorinidae)

by

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Abstract. The spawn masses of the littorinid *Bembicium vittatum* are clusters of gelatinous egg cases attached to the undersides of hard substrata, and can be found in many months of the year. Development is direct, with embryos developing within the egg cases through a larval veliger stage and hatching as crawling, benthic juveniles after approximately 3 weeks. These juveniles grow from an initial width of 0.5 mm to 2.0 mm in about 100 days under laboratory conditions. In the field, small snails grow rapidly from 2.0 mm to 8.5 mm, the size of the smallest sexually active snails, in about 260 days. Therefore, *B. vittatum* has an extended breeding season and direct development, and can grow to the size of sexually active snails within a year.

INTRODUCTION

The Australian littorinid genus *Bembicium* Philippi, 1846 includes five species: *B. auratum* (Quoy & Gaimard, 1834), *B. flavescens* (Philippi, 1851), *B. melanostoma* (Gmelin, 1791), *B. nanum* (Lamarck, 1822), and *B. vittatum* Philippi, 1846 (Reid, 1988). Members of this genus are abundant in the intertidal zones of sheltered and moderately exposed rocky shores, sand and mud flats, estuaries, salt marshes, coastal lagoons, and mangroves along the coasts of the Australian mainland, Tasmania, Norfolk Island, and Lord Howe Island. Differences in the habitats occupied by the different species of *Bembicium* result in virtually absolute ecological segregation of the individual species (Reid, 1988). The size, shape, coloration, and sculpture of shells show great variation within and between species in the genus *Bembicium*. Much of this variation occurs on a geographic scale, and variation within populations at individual localities is considerably less (Reid, 1988). Variation within local populations may sometimes, however, be as great as that between isolated populations (Anderson, 1958).

In the genus *Littorina*, those species with direct, non-

planktotrophic development show greater degrees of interpopulation variability for shell characteristics (Reid, 1988) and allozymes (Ward, 1990) than those species with planktonic veliger larvae. For *Bembicium*, there is little direct evidence about embryonic development and larval dispersal. All five species deposit spawn masses attached to a hard substratum (Reid, 1988). Based on characteristics of the protoconch, Reid (1988) concluded that *B. auratum* and *B. nanum* have planktotrophic larvae, but that *B. flavescens*, *B. melanostoma*, and *B. vittatum* spend little, if any, time in the plankton. Anderson (1958) observed development past the veliger stage within the egg capsules of *B. vittatum* (referred to as *B. melanostoma*), but the juveniles did not emerge from the capsules, so it is not certain that development was normal.

Consistent with an hypothesis of direct development, an electrophoretic study of enzyme polymorphisms in *B. vittatum* revealed substantial genetic differences among populations separated by short distances (Johnson & Black, 1991). However, populations from relatively exposed habitats were genetically more uniform, raising the possibility of a planktonic stage. The purpose of this study is to provide direct evidence on the early development of *B. vittatum* and on the growth of juveniles up to the size of sexual maturity, so that these important aspects of the life history can provide the context in which to interpret other information on the ecology and population genetics of this species.

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Table 1

Summary of locations and time of collection of spawn masses at the Pelsaert Group, Houtman Abrolhos Islands, in 1992.

Site	Number of spawn masses developing in the laboratory		
	April	June	September
Western exposed shore			
Gun Island	1	3	
Middle Island	4	2	
Eastern protected shore			
Burnett Island		2	5
Pelsaert Island (Noddy shore)	1	8	
Lakes			
Jackson Island			1
Pelsaert Island (Guano Lake)		6	
Pelsaert Island (N. Guano Lake)		1	

MATERIALS AND METHODS

We collected spawn masses of *B. vittatum* in the high intertidal zone at several different times of the year in the Houtman Abrolhos Islands (29°S, 114°E), Western Australia, the northern limit of the species' distribution. Our collections represented the three habitats sampled in the electrophoretic study by Johnson & Black (1991) (Table 1). In the laboratory, these spawn masses were maintained in small covered jars containing about 10 mL of seawater which was changed every 3–7 days. Room temperature was in the range 21–26°C, and the lights were on constantly. The spawn masses were examined regularly, and important features of the spawn masses, embryos, larvae, and juveniles were recorded. With an ocular micrometer, we measured the size of hatched but dead juveniles showing no signs of growth to estimate the size of the shell at hatching. Once the juveniles had hatched, we measured the width of the shells of up to 20 individuals per spawn mass, or all the survivors, on each examination of the cultured snails. Observations of each spawn mass ceased only when all the juveniles that hatched died, an average of 118 days after hatching (range 19 to 382 days).

In the field, we individually marked small *B. vittatum* by placing them aperture-down on a smooth surface and spraying them with Taubmans® enamel paint. Because of the pyramidal shape of the snails, new growth of the shell appears along the margin of the shell and, upon recapture, the initial and final width of the snail can be measured easily, providing direct evidence about rate of growth. We obtained 354 measurements of growth from snails that were less than 6 mm wide when we marked them, and that were recaptured after periods of 63 to 479 days. With the information on the number of days between marking and recapturing the snails and their initial and final widths, we used the Nonlinear Fit component of the computer program JMP® Version 2.0.5 for the Macintosh to fit a von Bertalanffy growth curve for *B. vittatum*. After checking that plots of the final size against the initial size for snails recaptured after the same number of days were not curvilinear and therefore were appropriate for a von Bertalanffy growth model, we obtained an estimate of the parameters, width_∞ (asymptotic width), and *K* (growth rate), by fitting the equation.

$$\text{final width} = (\text{width}_{\infty} - \text{initial width}) \cdot (1 - e^{(-K \cdot t)})$$

where *t* was the interval between marking and recapture expressed in years.

At the Noddy Shore site at Pelsaert Island, we measured the sizes of a population sample of snails and of copulating pairs of *B. vittatum* in April 1992 and 1993. We assumed that the snail with its penis inserted into its partner's mantle cavity was the male, although by dissecting copulating pairs, Saur (1990) found that 7% of mating pairs in one species of littorine and 27% in another were both males. We combined the information from these data to determine the minimum sizes of male and female snails that engage in mating activity.

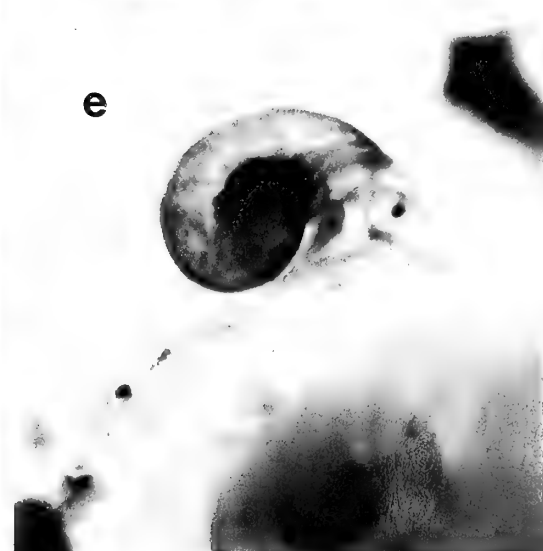
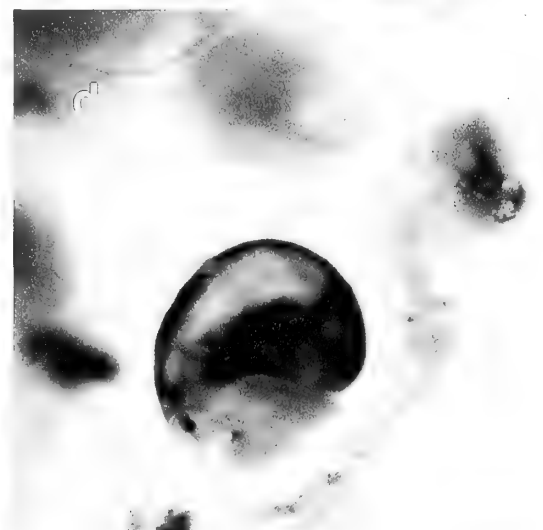
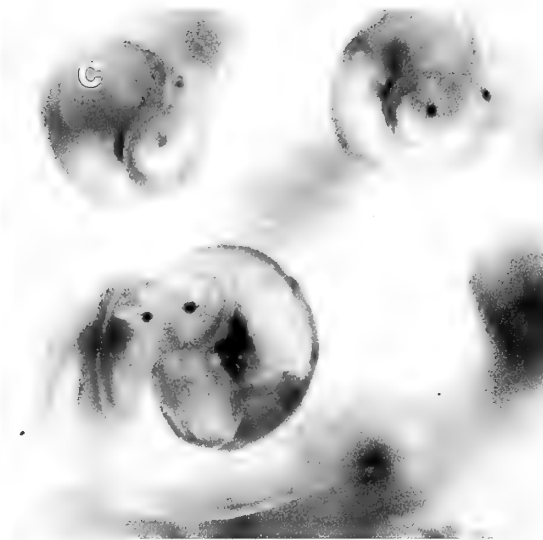
RESULTS

Spawn

The sexes are separate in *B. vittatum*, the males being distinguished by the presence of a penis located anterior to and beneath the right tentacle, and fertilization is apparently internal. At several intertidal localities in the Houtman Abrolhos Islands, we observed spawn masses of *B. vittatum* attached directly to surfaces in crevices in the undersides of rocks and pieces of dead wood. We found

Figure 1

Developmental stages of *Bembicium vittatum* observed under laboratory conditions. a) Close-up view of an oval-shaped, gelatinous case of embryos. Each embryo is contained within an ovoid envelope about 0.5 mm maximum diameter. b) A spawn mass of four cases of juveniles just about to hatch. The cases are about 3 mm in length. c) A veliger larva inside an envelope and surrounded by the gelatinous matrix of the case. The velar lobes, eye spots, and tentacles are visible. d) A juvenile before hatching, crawling within the envelope. The velum has been resorbed, the foot is well developed, and the shell has become more pigmented. e) A juvenile after hatching, crawling on the outside of the case.



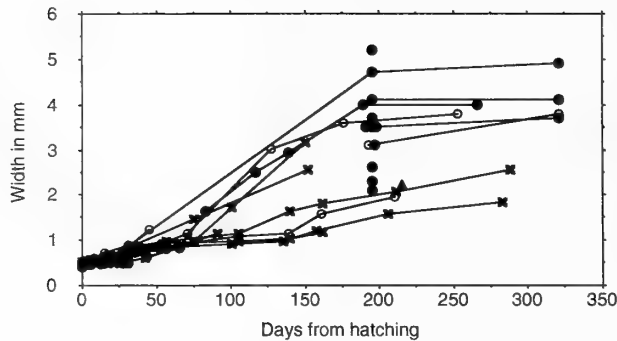


Figure 2

Growth of juvenile *Bembicium vittatum* hatched from spawn masses collected in the field and reared in the laboratory. The symbols represent the habitat where the spawn masses were collected: open circles—Eastern Shores, closed circles—Western Shores, crosses—Lakes, closed triangle—laboratory. Lines join the mean widths of juveniles from the same spawn mass. At 195 days from hatching, superimposed points at 3.1 and 3.5 mm are offset along the x axis for clarity.

numerous masses of spawn attached to rocks in all three habitats examined in January, April, June, and September, and in the laboratory in November, suggesting that breeding occurs throughout most of the year.

Each spawn mass consisted of clusters of closely packed, transparent, oval-shaped, gelatinous cases, each 2.5–5.0 mm in length (mean = 3.5 mm, SE \pm 0.12, n = 31) and 1.5–2.8 mm in width (mean = 2.0 mm, SE \pm 0.06, n = 31) (Figure 1a, b). Each case contained 10–58 creamy white, yolky embryos (uncleaved embryos average 245 μ m (SE \pm 5, n = 22) in diameter). Each embryo was enclosed in a transparent ovoid envelope, measuring 460–720 μ m in length (mean = 565 μ m, SE \pm 3, n = 251) and 360–600 μ m in width (mean = 490 μ m, SE \pm 3, n = 251).

Early Development to Hatching

The eggs in each case developed simultaneously, undergoing the typical prosobranch development, including a trochophore stage and a veliger stage. The veligers are characterized by: a yolky visceral hump covered by a dextrally coiled, smooth, unsculptured, pale brown, transparent shell; a small ciliated bilobed velum; a pair of prominent black eye spots; a small foot and colorless operculum (Figure 1c). The velar lobes, although ciliated, produced only slow rotation of the veligers within their envelopes.

Spawning was not observed in the field and therefore the time of development can only be estimated from the laboratory observations. Hatching occurred within 3 weeks of collection. There was no evidence of a planktonic larval stage, the embryos hatching as fully metamorphosed, free-living, crawling, benthic juveniles (Figure 1d, e). The rate of development of the embryos was not uniform throughout the spawn masses, and the juveniles from any one spawn

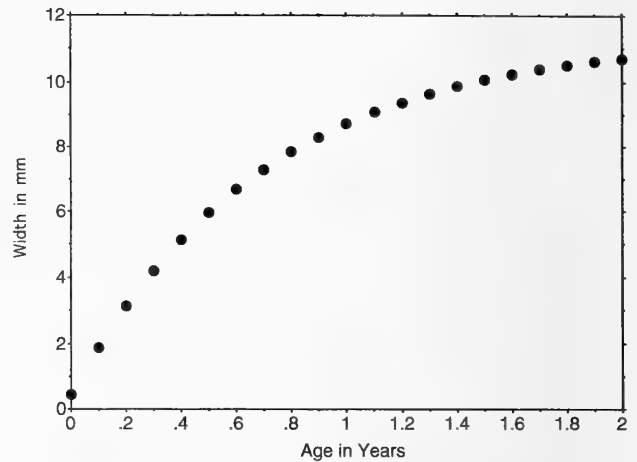


Figure 3

Predicted width of *Bembicium vittatum* growing according to a von Bertalanffy growth equation: width = 11.4 (1 - $e^{1.41(\text{years} - 0.45)}$). The parameters were estimated using observations on 354 juvenile snails marked when they were 2–6 mm in width and recaptured after intervals of 63 to 479 days.

mass hatched over a period of several days. This may have arisen because all the cases were not spawned simultaneously or because the rate of development within the interior of a spawn mass was slower than at the periphery.

During the late veliger period, prior to hatching, by which time most of the yolk reserves were almost completely utilized, the larvae developed a pair of tentacles lateral to the eye spots, the shell increased in size and became distinctly brown, the velar lobes were resorbed, and the foot became faintly pigmented, elongated, muscular, and highly mobile (Figure 1d, e).

The juveniles actively crawled within their envelopes prior to hatching. Recently produced spawn masses were quite firm, but they began to soften and disintegrate as the juveniles started to hatch. The newly hatched, crawling juveniles had a shell 1.25 whorls in size, with an average width of 450 μ m (SE \pm 3, n = 187). The shell aperture was straight edged. There was no evidence for a larval beak or sinusigera notch extending anteriorly into the aperture of the larval shell, a characteristic of indirectly developing planktonic larvae.

Growth of Juveniles in the Laboratory

Although substantial posthatching mortality of juveniles occurred in the laboratory, we observed feeding and growth very soon after hatching, and a small number of juveniles lived for extended periods. Growth rates were variable among the juveniles from different spawn masses, but after 7 months in the laboratory, juveniles fed on films of the microalgae *Pavlova lutheri* (Droop) Green had grown to 4.0–5.0 mm wide, with 4–5 whorls. The characteristic features of the adult shells, including the flat-based tro-

choidal or conical shape with a telonch sculptured by spiral grooves and radial folds, were evident.

Figure 2 shows four important features in the time course of the increase in width of shell of juveniles in the laboratory starting from the day of hatching. First, on average, the width of the shell at hatching was 0.45 mm, ranging from 0.39 to 0.53 for averages from each of 22 spawn masses. Second, the growth rates of the juveniles were variable, but the snails hatched from spawn masses from each of the three habitats (Table 1) were interspersed over the whole range of rates up to about 140 days. After that, the size of clutches from the lakes was smaller than that of clutches from western shores (150–195 days) and from both western and eastern shores (>250 days) as judged by analyses of variance and post hoc pairwise tests. Third, the fastest growing juveniles in the laboratory reached about 2.0 mm in width after about 100 days. Finally, the rate of growth of the faster growing snails seemed to level off after about 200 days, at a width of 3 to 5 mm.

Growth of Juveniles in the Field

Of the 354 snails that we recaptured that were less than 6.0 mm wide when we marked them, six were initially less than 2.5 mm (minimum, 1.6; average, 2.0 mm). These six snails grew at an average of $0.026 \text{ mm} \cdot \text{day}^{-1}$, which would make them 4.5 mm wide in 96 days. Thus, these snails in the field grew at rates comparable to those of the fastest growing juveniles in the laboratory (Figure 2). Therefore, assuming that 2.0 mm snails from the field were about 100 days old, they would reach 4.5 mm in width when about 200 days old.

In the laboratory, even the fastest growing snails failed to increase in width much past 5 mm at 200 days of age (Figure 2). This was not the case for juvenile snails in the field. We recaptured 115 snails that were marked when they were between 4.0 and 4.9 mm wide (mean of 4.5 mm). Although we recaptured these snails at intervals up to 367 days after they were marked, the final size they reached did not increase after 208 days, and their mean final widths ranged between 8 and 10 mm. On average, the snails recaptured after intervals of 208 days or less grew at a rate of $0.025 \text{ mm} \cdot \text{day}^{-1}$. Thus a 4.5 mm snail would reach 9.5 mm in 200 days.

As a second approach to analysis of growth rates, we fitted a von Bertalanffy growth curve to the data from all 354 *B. vittatum* that were less than 6.0 mm when marked. The estimates and the approximate standard errors of the parameters of the von Bertalanffy growth curve were $\text{width}_{\infty} = 11.4 \pm 0.62 \text{ mm}$ and $K = 1.41 \pm 0.194$. Figure 3 shows the size-at-age of *B. vittatum* predicted by the von Bertalanffy for increments of 0.1 year up to 2 years. From a size of 0.45 mm at hatching, *B. vittatum* growing according to this model would reach a width of 8.7 mm after one year and 9.5 mm after 1.25 years.

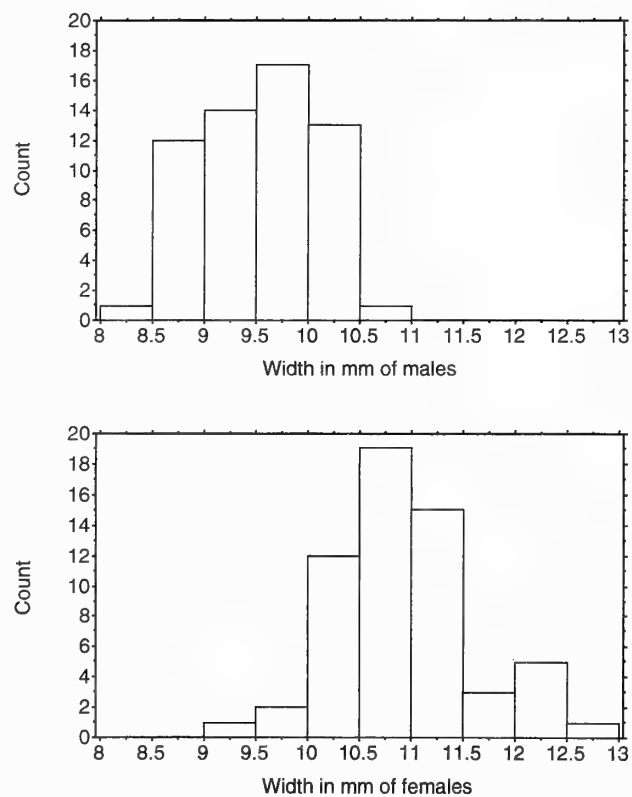


Figure 4

Size frequency distributions of 58 mating pairs of *Bembicium vittatum* observed at Noddy Shore, Pelsaert Island, Houtman Abrolhos Islands in April 1992 and April 1993.

Sizes of Mating Pairs

We collected 44 copulating pairs of *B. vittatum* at the Noddy Shore site on Pelsaert Island in April 1992, and 14 pairs in April 1993. In all pairs but one, the male was smaller than the female, the difference in size ranging up to almost 3 mm. As Figure 4 shows, the distribution of sizes of mated animals was sharply truncated at the left of the size distribution, suggesting that the minimal sizes of sexual activity were about 8.5 mm for males and about 10.0 mm for females. In both years, the population of snails at the site included many individuals that were slightly smaller than the ones found mating, so our measurements should accurately indicate the minimum size at which mating activity occurs and indirectly estimate the size at maturity.

DISCUSSION

Our observations confirm the descriptions of the spawn masses of *B. vittatum* given by Anderson (1958), and also establish that the embryos are not planktotrophic. Development ended in the hatching of crawling, benthic juveniles from the cases. The yolk provisioned in the eggs of *B.*

vittatum was clearly sufficient for complete development within the envelopes, without the requirement for external food sources. Mileikovsky (1975) reported that a small number of littorinids display poecilogony, in which there are different types of larval development in local populations from different parts of the geographical range of a species. More recently, Bouchet (1989) considered all the alleged examples of poecilogony in prosobranchs and shelled opisthobranchs and concluded that the phenomenon did not exist in these groups, including the littorines. Most formerly accepted examples are now known to involve cryptic species. We found no evidence for poecilogony with *B. vittatum*. Spawn masses were found consistently from the three kinds of habitats at the Houtman Abrolhos Islands, and embryonic development was the same regardless of habitat of origin. This confirmation of direct development is consistent with the high levels of genetic subdivision found in *B. vittatum*, but leaves open the question of why smaller genetic differences were found among populations from the more exposed habitat (Johnson & Black, 1991). The absence of a planktonic stage also raises the question about the origin of this disjunct group of populations in the Houtman Abrolhos Islands, which are 400 km north of the nearest population (Reid, 1988).

In the two related species, *B. auratum* and *B. nanum*, the embryos hatch after 10–12 days as planktotrophic veligers which probably spend several weeks in the plankton before settlement and metamorphosis (Anderson, 1958; Anderson, 1961, 1962; Murray, 1964). The eggs of *B. auratum* and *B. nanum* are smaller (120 μ m and 100 μ m diameter, respectively) and more numerous (60–100 and 100–200 eggs) (Anderson, 1961, 1962) than those produced by *B. vittatum* (Anderson, 1958; this study). Anderson (1958) reported that the irregularly shaped spawn masses of *B. melanostoma* (= *B. vittatum*) contained 8–30 eggs, with an average diameter of 172 μ m (range = 149–197 μ m), in hyaline envelopes averaging 460 μ m (range = 413–512 μ m) in length and 404 μ m (range = 358–451 μ m) in width. Our observations on *B. vittatum* were that the early embryos and their envelopes were slightly larger than the ones described from South Australia by Anderson. The relatively large eggs of *B. vittatum* provide sufficient nutrient resources for the embryos to develop into juveniles before leaving the envelopes, whereas by the time the embryos of *B. auratum* and *B. nanum* develop into the veliger stage, the majority of the yolk has been utilized, and the veligers hatch into the plankton (Anderson, 1958).

A range of reproductive types is found within the gastropod family Littorinidae, members of which inhabit the supralittoral and littoral zones of shores throughout the world. Some species are viviparous; other lay benthic egg masses which may give rise to either planktonic larvae or benthic juveniles, but the majority [28 of the 39 species reviewed by Mileikovsky (1975)] possess a completely pelagic development, producing planktonic egg capsules and passing through a free-swimming veliger stage before be-

coming benthic. The early life histories of the species within the genus *Bembicium* are thus of particular interest because among other littorinids, the hatching of planktotrophic veligers from benthic egg masses (as in *B. auratum* and *B. nanum*) is rare, being documented in only two other species [*Risellopsis varia* (Hutton, 1873) and *Lacuna vineta* (Montagu, 1803)], and few other species have been confirmed to undergo direct development similar to *B. vittatum* (Mileikovsky, 1975; Reid, 1988). *B. vittatum* is very closely related to the two species *B. flavescens* and *B. melanostoma* (Reid, 1988). Based on the morphology of their shells, these three have in the past been considered synonymous, but are now separated because of consistent differences in penial shape and the reproductive isolation that implies (Reid, 1988). However, there is no information regarding the early development of these two species. Reid (1988), from an examination of the protoconchs of *B. flavescens* and *B. melanostoma*, considered that they may similarly undergo direct development in benthic spawn masses, and he suggested that the lack of a planktonic stage could explain their potential for isolation and allopatric speciation.

Our observations on the growth of hatchlings in the laboratory and small snails in the field also established important aspects of the early life history of *B. vittatum*. The early growth in the laboratory helped set the range of possible rates of growth for the extremely small snails that were impossible to mark and recover in the field. The similarity in rate of growth of the snails from 2.0 to 4.5 mm width in the laboratory and in the field reinforced the estimate of the length of time it takes snails to reach a size where we obtained sufficient samples from the field to estimate rates of growth for the larger snails. Both the raw data on growth of small snails and the summary provided by the fitting of the von Bertalanffy growth model to those data showed clearly that *B. vittatum* can reach a size of at least 8.5 mm within their first year of life.

The width of 8.5 mm was important for another reason because it was the minimum size of the male snails that we found copulating. However, males were almost always smaller than their female partners. There may be several explanations for this difference between males and females in minimum size of mating animals. Females may grow faster than males and so be larger at the same age, or females may take longer to mature and so be older and larger when they begin mating. Only future observations of rate of growth by snails of each sex will revolve which of these alternatives or others is correct. Nevertheless, the information on sizes of mated pairs, together with our knowledge of rates of growth, indicates that many snails become sexually active in about a year from when they hatched and therefore provides an estimate of the minimum generation time of this snail.

In combination, the information on the occurrence of spawning in the field, the mode of reproduction, estimates of the rate of growth and the size of sexually active indi-

viduals provides a clear picture of the early life history of this snail. At the Houtman Abrolhos Islands, *B. vittatum* is a species with overlapping generations and an extended breeding season. This is the essential context in which to interpret past (Johnson & Black, 1991) and future information about population genetics and ecology of this species and firmly fixes the temporal scale in which patterns of genetic divergence must act.

ACKNOWLEDGMENTS

We thank B. Marinovic for providing the algal cultures, and M. Stuckey for assistance in rearing the juveniles in the laboratory. This work was supported by a grant from the Australian Research Council, and is a contribution from the Marine Biological Laboratory of The University of Western Australia.

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A New Species of the Volutid Gastropod *Fulgoraria* (*Musashia*) from the Oligocene of Washington

by

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Abstract. A new species of volutid gastropod, *Fulgoraria* (*Musashia*) *ellenmooreae*, is present throughout Oligocene deep-water strata in western Washington. Previous workers reported but did not formally name the new species from the Blakeley Formation near Seattle and from the Lincoln Creek Formation in southwestern Washington. It is herein reported for the first time from the Makah and Pysht Formations along the north side of the Olympic Peninsula. This new species represents one of the earliest known records of subgenus *Musashia* in the world and is unusual among fulgorariine volutids because of its large protoconch, well-developed siphonal fasciole, and almost smooth sculpture. Its closest relatives are *F. (M.) nagaii* Shikama from the upper Oligocene to lower Miocene of northern Japan and *F. (M.) olutorskiensis* (Krishtofovich) from the Oligocene of northeastern Kamchatka Peninsula, Russia.

INTRODUCTION

The volutid gastropod genus *Fulgoraria* Schumacher, 1817, and its subgenus *Musashia* Hayashi, 1960, are restricted today to warm to temperate waters in Japan and its adjacent seas (Shikama, 1967) at bathyal depths most commonly between 200 and 750 m (Oleinik, 1993:fig. 20). During the Cenozoic, *Fulgoraria* was more widespread than today, and species were especially common in bathyal environments during the Oligocene on both the eastern and western margins of the north Pacific Ocean (Oleinik, 1993). The earliest known *Fulgoraria* in the world is *F. (Psephaea) zinsmeisteri* Mount, 1976 from the upper Paleocene of Simi Valley, Ventura County, southern California (Mount, 1967).

Moore (1984a) reported that the earliest known species of *Musashia* is probably *Musashia* (*Nipponomelon*?) *caucasica* (Korobkov, 1949:694–695, text figs. 1, 2; 1955:205–206, pl. 4, figs. 6, 6a) from the middle Eocene in the Caucasus of Russia. Illustrations of the holotype show that it is poorly preserved with unclear morphology, and the holotype is missing from the paleontological collections at

the University of St. Petersburg, Russia (A. E. Oleinik, personal communication). The earliest undoubted records of *Musashia* in the eastern Pacific and in the world are *F. (Musashia) weaveri* (Tegland, 1933) and *F. (Musashia) ellenmooreae* sp. nov. Both are from rocks as old as early Oligocene in Washington. It is the purpose of the present paper to describe this new species, which has been recognized before but not formally named. In addition, we report it, for the first time, from the north side of the Olympic Peninsula, Washington (Figure 1).

The molluscan zones used in this report stem from Durham (1944) who proposed the *Echinophoria rex* (Tegland, 1931) and *Echinophoria apta* (Tegland, 1931) Zones, and from Armentrout (1975) who proposed the *Echinophoria fax* (Tegland, 1931) Zone. Moore (1963) subsequently assigned *E. fax*, *E. rex*, and *E. apta* to *Liracassis*; however, Moore (1984b) later referred to *E. fax* as “*Echinophoria*” *fax*.

The molluscan stages used in this report stem from Armentrout (1975) and Addicott (1976). The former worker proposed the Galvinian and Matlockian Stages, and the latter worker proposed the Juanian and Pillarian

Stages. The chronostratigraphic relationships between the molluscan zones and molluscan stages used in this report are shown in Figure 2.

Abbreviations used for catalog and/or locality numbers are: JLG, James L. Goedert field locality; LACMIP, Natural History Museum of Los Angeles County, Invertebrate Paleontology Section; UCMP, University of California Museum of Paleontology (Berkeley); USGS, United State Geological Survey, Menlo Park, California; UWBM, University of Washington (Seattle), Thomas Burke Memorial Washington State Museum (= UW in older literature).

STRATIGRAPHIC DISTRIBUTION AND GEOLOGIC AGES

Durham (1944) reported, under the name of *Mioleionea* sp. A, several poorly preserved specimens of the new species from UCMP locs. A1803, A1804, A1807, and A1812 from the *Echinophoria rex* (now *Liracassis rex*) Molluscan Zone in the Blakeley Formation on and near Bainbridge Island and at Seattle, Washington (Figure 1). The *L. rex* Zone is correlative to most of the lower Oligocene (Figure 2).

Armentrout (1973:339) reported specimens of the new species from 12 localities in the Lincoln Creek Formation, Satsop River area, approximately 50 km northwest of Olympia, Washington (Figure 1). The stratigraphically lowest locality is UWBM loc. B0356, and the stratigraphically highest locality is UWBM loc. B0406 (Figure 2). Armentrout (1973) reported that the stratigraphic range of the new species in the Satsop River area corresponds to the "*Echinophoria*" fax, *L. rex*, and *L. apta* Zones. Prothero & Armentrout (1985), who refined the age of the Eocene/Oligocene boundary by means of magnetostratigraphic studies of the Lincoln Creek Formation in the Satsop River area, correlated the "*E.*" fax Zone with the lowermost Oligocene, the *L. rex* Zone with the rest of the lower Oligocene, and the *L. apta* Zone with the upper Oligocene (Figure 2). It is important to mention that Armentrout (1973:pl. 6, figs. 10, 13) found, within the stratigraphic range of the new volutid in the Lincoln Creek Formation in the Satsop River area, forms of *L. rex* transitional to *L. apta*. The presence of these transitional forms indicates an age of latest early Oligocene to earliest late Oligocene. The siltstones that contain the new species in the Lincoln Creek Formation in the Satsop River area also contain benthic foraminifera that are indicative of open-sea conditions in cool- to cold-water temperature at upper bathyal depths (Rau, 1966).

Moore (1984a, b) reported several specimens of the new species from the upper Lincoln Creek Formation near Knappton, in the proximity of the mouth of the Columbia River, southwestern Washington (Figure 1). In this area, the formation consists of poorly bedded, dark gray siltstone with scattered fossiliferous concretions that are argillaceous and resistant. The outcrops are in landslide scarps on hillsides and on a tidal flat accessible only during ex-

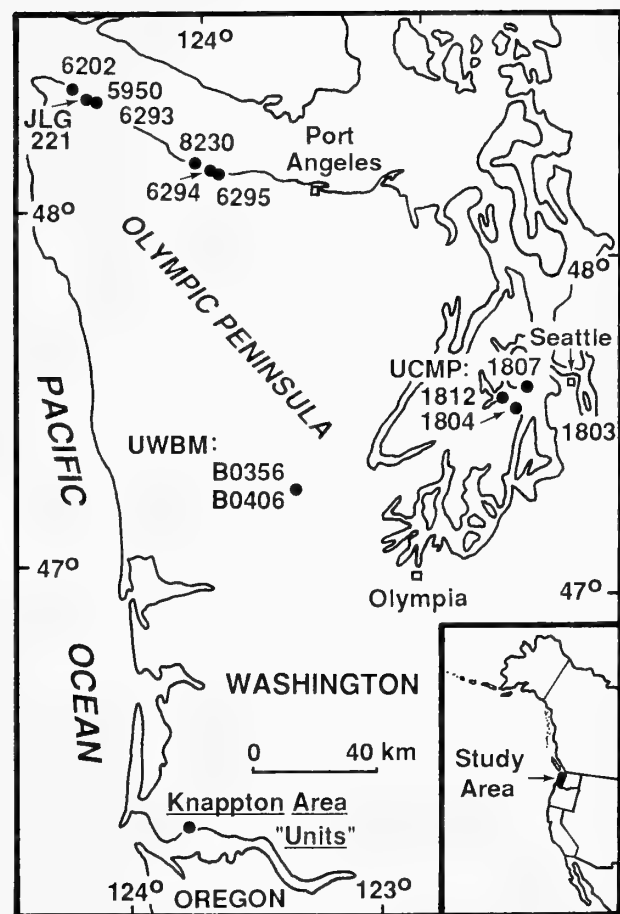


Figure 1

Index map to localities of *Fulgoraria (Musashia) ellenmooreae* Squires & Goedert, sp. nov. Unless otherwise indicated, localities are LACMIP localities.

treme low tides. The resistant fossiliferous concretions erode out of the toes of landslides and beach-terrace exposures and accumulate along the shoreline. Beginning in the late 1970s, J. L. and G. H. Goedert extensively collected these concretions and grouped them in relation to where they were collected along the shoreline. They established four informal groupings (units 1 through 4) of the float concretions, with each successively higher number roughly corresponding to a stratigraphically higher part of the formation. We herein use quote marks with these field "units" because they are not true stratigraphic units. The Goedert collection was sent to LACMIP where it was subsequently studied by Zullo (1982), Rigby & Jenkins (1983), and Moore (1984a, 1988).

A diverse assemblage of fossils is associated with the upper part of the Lincoln Creek Formation in the Knappton area. There are benthic foraminifera, solitary corals, siliceous sponges brachiopods, scaphopods, many gastropods (including *Bathybembix*) and bivalves, nautiloids (in-

cluding many *Aturia* specimens), sepiids?, decapods, spatangoids, barnacles (including many arcoscappelids), shark teeth, mammal bones, and *Tisoo* burrows (Zullo, 1982; Rigby & Jenkins, 1983; Moore, 1984a), as well as pteropods (Squires, 1989), the large isopod *Palaega goedertorum* Wieder & Feldmann, 1989, crinoid stems, starfish, and bored wood. The siliceous sponges indicate a paleoenvironment at depths of between 300 and 350 m (Rigby & Jenkins, 1983), and the other fossils indicate a similar depth range (Moore, 1984a).

Zullo (1982), Rigby & Jenkins (1983), and Moore (1984a) utilized the same four field "units" established by the Goederts. Zullo (1982:fig. 2) and Rigby & Jenkins (1983:fig. 2) gave a chronostratigraphic significance to the "units" and assigned "unit 1" to the late Eocene, "unit 2" to the early Oligocene, and "units 3 and 4" to the late Oligocene on the basis of barnacles. Moore (1984a:fig. 3) plotted a stratigraphic position for each "unit" and assigned all the "units" to the early Miocene on the basis of mollusks. Her focus of study was on "unit 4" (= LACMIP loc. 5842), and she reported that Juanian Stage fossils in this "unit" represent a rarely preserved *Liracassis apta* Zone fauna that is transitional between the well-known part (upper Oligocene) of the Juanian Stage and the Pillarian Stage (lower Miocene).

Based on our examination of these float concretions in the LACMIP collection, we found that the fauna of each "unit" is similar and that the new volutid is present in "units 1, 2, and 4." Specimens of the new volutid and of the age-diagnostic *Liracassis* are most common in "unit 4," where there are forms of *L. rex* transitional to *L. apta*. The presence of these transitional forms indicates an age of latest early Oligocene to earliest late Oligocene. It is important to mention that the fauna (including the transitional forms of the *Liracassis*, as well as the new volutid) found in the upper part of the Lincoln Creek Formation is very similar to that found at LACMIP locs. 6294 and 6295 in the lower Pysht Formation and LACMIP loc. 6293 from the upper Makah Formation. These three localities, which are discussed below, have yielded fossils indicative of an age of latest early Oligocene to earliest late Oligocene. Based on these faunal similarities, and pending a detailed biostratigraphic study of the *in situ* fossils in the Knappton area, we tentatively conclude that the age of the new species in the upper part of the Lincoln Creek Formation in the Knappton area is also latest early Oligocene to earliest late Oligocene (Figure 2).

Seven new stratigraphic localities are reported herein for the new species. All are on the north side of the Olympic Peninsula (Figure 1). Four of the localities are from the Makah Formation, and three are from the Pysht Formation (Figure 2). Assignment of each locality to its respective formation was based on a study of geologic maps by Tabor & Cady (1978) and by utilizing the stratigraphic refinements of Snaveley et al. (1977).

Three of the Makah Formation localities (JLG 221,

LACMIP 5950 & 6202) are from the Jansen Creek Member, a transported olistostromal rock unit containing mostly shallow-water marine conglomerate and fossiliferous sandstone enclosed in deep-water (1000 to 2000 m) marine siltstone and sandstone (Snaveley et al., 1980; Kaler, 1988: 17). Specimens of the new species from the Jansen Creek Member are uncommon, poorly to moderately well preserved, and associated with the gastropod *Bathybembix*. This genus is one of the most abundant elements in bathyal faunas around the Pacific margin today (Hickman, 1984). The nautiloid *Aturia* is also present at localities LACMIP locs. 5950 and 6202. According to Armentrout et al. (1983), the Jansen Creek Member is earliest Oligocene in age. Carole S. Hickman (personal communication) also assigned the rocks from the Jansen Creek Member localities to the earliest Oligocene and determined that the associated fossils definitely belong to a bathyal assemblage.

The other locality (LACMIP 6293) from the Makah Formation is in the middle of the formation and is in nearly barren mudstone and siltstone. This part of the formation corresponds to the bathyal environment that is pervasive throughout the formation (Snaveley et al., 1980). Only a few specimens of the new species were found at this locality, and they are well preserved. Associated fossils are rare specimens of a scaphopod, gastropods (including *Bathybembix*), bivalves, the nautiloid *Aturia*, and the large isopod *Palaega goedertorum*. *Palaega* lives today at depths ranging from about 310 to 1280 m (Holthuis & Mikulka, 1972). The rocks at this locality contain *L. rex* and specimens that look like *L. apta* (E. J. Moore, personal communication). The presence of these transitional forms indicates an age of latest early Oligocene to earliest late Oligocene.

The three localities (LACMIP 6294, 6295, 8230) in the lower part of the Pysht Formation are just west of the mouth of Murdock Creek and are in close proximity to each other. The type locality for the new species (LACMIP 6294) contains numerous and well-preserved invertebrates in small, discontinuous concretionary lenses of sandstone containing masses of shells surrounded by nearly barren mudstone. Sixteen specimens of the new species were found at LACMIP loc. 6294. They are well preserved, complete, and make up a partial growth series, ranging from 28 to 112 mm in height. Associated fossils are brachiopods, scaphopods, numerous gastropods and bivalves, the nautiloid *Aturia*, and the teeth of the shark *Heptanchias howelli* (Reed, 1946). The isopod *Palaega goedertorum* is rare in surrounding mudstone. Most of the fossils are complete, and those that are fragmentary show no evidence of rounding. Although the fossils have undergone some degree of post-mortem concentration into lens-shaped masses, the distance of transport was short. The mudstones surrounding LACMIP loc. 6294 contain mid-bathyal foraminifera (Hal Heitman, personal communication). The *Liracassis* specimens at this locality are forms of *L. rex* transitional to *L. apta*, and the presence of these transitional forms

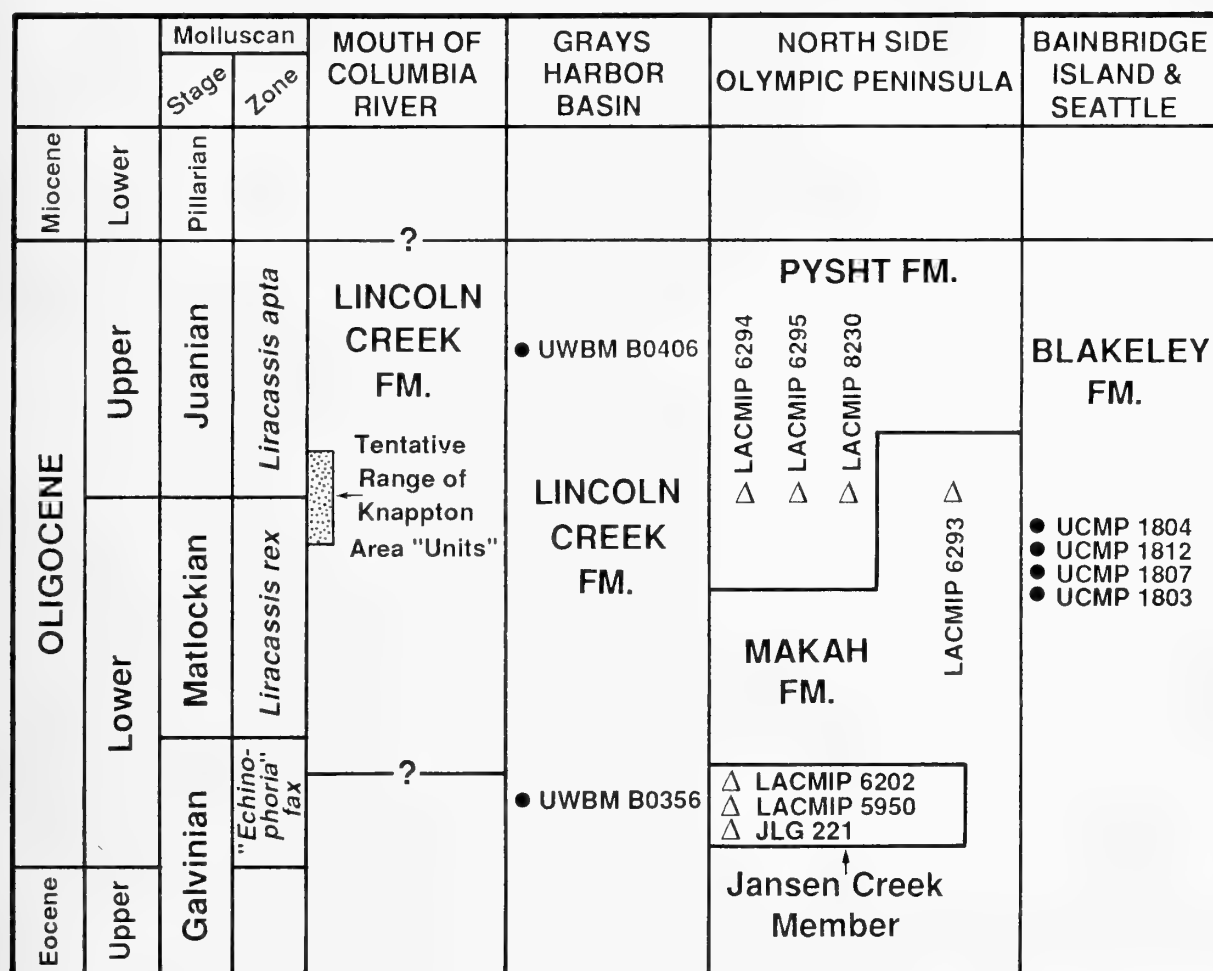


Figure 2

Chronostratigraphic chart showing position of previously known localities (black dots) and new localities (open triangles) for *Fulgoraria* (*Musashia*) *ellenmooreae* Squires & Goedert, sp. nov. For the Lincoln Creek Formation in the Grays Harbor area, only the stratigraphically lowest and highest localities are shown. Correlation of molluscan stages and zones versus geologic time is derived from Moore (1984b, fig. 6) and Prothero & Armentrout (1985: figs. 2, 3).

indicates an age of latest early Oligocene to earliest late Oligocene.

At LACMIP loc. 6295, fossils are rare in concretions found as float derived from mudstone and siltstone in beach cliffs and the beach terrace in the vicinity of LACMIP loc. 6294. A few specimens of the new species were found, and they are moderately well preserved. Associated fossils are a scaphopod, gastropods and bivalves, pteropods (Squires, 1989), the nautiloid *Aturia*, the isopod *Palaega goedertorum*, and rare leaves and wood. Rocks in this vicinity have also yielded a bird (Olson, 1980) and a diverse assemblage of primitive cetaceans (Goedert, 1988:100). Squires (1989) reported that the fossils at LACMIP loc. 6295 consist of a mixed assemblage with most of the re-

mains apparently derived from deep-water, low-diversity benthic communities. Foraminifera from rocks in the vicinity of LACMIP loc. 6295 indicate that deposition probably took place at a depth of between 300 and 2000 m (Rau, 1964). Olson (1980) and Squires (1989) assigned this part of the Pysht Formation a late Oligocene age, whereas Goedert & Squires (1993) tentatively assigned it an early Oligocene age. The age of the locality is herein refined to the same age as the rocks at locality 6294; namely, an age of latest early Oligocene to earliest late Oligocene.

At LACMIP loc. 8230, only a single specimen of the new species was found, in float. The only associated fossil was an articulated specimen of the solemyid bivalve *Acha-*

rex. These float specimens are undoubtedly the same age as the specimens collected from nearby LACMIP locs. 6294 and 6295.

The age of the Pysht Formation just west of the mouth of Murdock Creek at LACMIP locs. 6294, 6295, and 8230 is older than generally reported for this formation. Armentrout et al. (1983) reported the age of the entire Pysht Formation as late Oligocene and earliest Miocene. The age of the lower part of the Pysht Formation was discussed by Domning et al. (1986) who tentatively assigned slightly higher strata an age of "middle" of late, but not latest, Oligocene. All three localities are near the base of Durham's (1944) reference section of the *L. rex* Zone (early Oligocene). Because forms of *L. rex* transitional to *L. apta* are present in the lower part of the Pysht Formation west of Murdock Creek, the age of this part of the formation is latest early Oligocene to earliest late Oligocene.

Mixed with the concretions at LACMIP loc. 6295 and near loc. 8230 are rare blocks of micritic limestone, up to 1 m across, with articulated specimens of the bivalves *Calyptogena* (*C.*) *chinookensis* Squires & Goedert, 1991, *Thyasira* sp., and *Modiolus* (*M.*) *willapaensis*(?) Squires & Goedert, 1991. Goedert & Squires (1993) interpreted these bivalve associations as cold-methane-seep communities.

SYSTEMATIC PALEONTOLOGY

Class Gastropoda Cuvier, 1797

Family VOLUTIDAE Rafinesque, 1815

Subfamily FULGORARIINAE Pilsbry & Olsson, 1954

Discussion: The higher systematics of this subfamily are not fully resolved. The most recent revisions (Shikama, 1967; Weaver & du Pont, 1970) differ primarily in the ranking of supraspecific taxa, and the reader is referred to Oleinik (1993) for a complete listing of these taxa. Shikama (1967), using only shell characters, recognized three genera: *Fulgoraria* Schumacher, 1817, *Musashia* Hayashi, 1960, and *Saotomea* Habe, 1943. He also recognized four subgenera of *Musashia*: *Musashia* s.s., *Nipponomelon* Shikama, 1967, *Mioleionea* Dall, 1907, and *Neopsephaea* Takeda, 1953. Weaver & du Pont (1970), using both shell and radular characters, recognized only the genus *Fulgoraria*, with several subgenera, including *Musashia*. They considered *Nipponomelon* to be a synonym of *Musashia*. The present paper follows the more modern classification of Weaver & du Pont (1970).

Genus *Fulgoraria* Schumacher, 1817

Type species: *Fulgoraria chinensis* Schumacher, 1817 = *Voluta rupestris* Gmelin, 1791, by original designation, Recent, Taiwan.

Subgenus *Musashia* Hayashi, 1960

Type species: *Voluta hirasei* Sowerby III, 1912, by original designation, Recent, south coast of Japan.

Fulgoraria (*Musashia*) *ellenmooreae*

Squires & Goedert, sp. nov.

(Figures 3–8)

Mioleionea sp. A Durham, 1944:178.

Musashia (*Musashia*) *evelyni* [MS Name] Armentrout, 173: 338–339, pl. 5, figs. 25, 27, 28.

Musashia (*Musashia*) n. sp. Moore, 1984a: 18, figs. 62, 65, 76, 80, 87; 1984b: table 1.

Diagnosis: A *Musashia* with a large low protoconch, a moderately short spire, an inner lip with two subequal folds, almost smooth sculpture, and a well-developed siphonal fasciole.

Description: Shell of medium to moderately large size, up to 112 mm in height, fusiform, moderately high spired, apical angle about 27 degrees. Body whorl composing about 82% of shell height. Protoconch of about 1.5 whorls, large, rounded, low, and smooth. Teleoconch of about five whorls. Suture moderately inclined and slightly impressed. Penultimate and body whorl almost smooth except for faint spiral lines. Teleoconch surface with microscopic growth striae that bend abaperturally near suture. Subsutural band obsolete. Inner lip covered by a thin callus and with two subequal folds. Outer lip thickened. Siphonal fasciole well developed. Aperture narrow, with a siphonal notch.

Holotype: LACMIP 12274.

Type locality: LACMIP loc. 6294, near mouth of Murdock Creek, latitude 48°09'37"N, longitude 123°52'28"W.

Paratype: LACMIP 12275, also from LACMIP loc. 6294.

Dimensions: Of holotype, height 70.3 mm, width 25.2 mm; of paratype, height 84.4 mm, width 30 mm.

Discussion: Certain specimens of the new species have less elongate upper spire whorls relative to other specimens from the same locality. An example is the holotype (Figures

Explanation of Figures 3 to 8

Figures 3–8. *Fulgoraria* (*Musashia*) *ellenmooreae* Squires & Goedert, sp. nov., LACMIP loc. 6294, Pysht Formation, north side of Olympic Peninsula, Washington. Figures 3–6: holotype LACMIP 12274. Figure 3: apertural view, $\times 1.6$. Figure 4: abapertural view, $\times 1.6$. Figure 5: oblique apertural view showing the two plaits on the inner lip, $\times 1.6$. Figure 6: magnified oblique apertural view showing the two plaits on the inner lip, $\times 3.5$. Figures 7–8: paratype, LACMIP 12275, $\times 1.1$. Figure 7: apertural view. Figure 8: abapertural view.



3–5), whose antepenultimate whorl is less elongate than that of the paratype (Figures 7, 8).

Specimens of the new species from the Jansen Creek Member (LACMIP locs. 5950, 6202 and JLG loc. 221) have a shorter spire and are smaller in size than most of the other studied specimens of the new species. These specimens are indistinguishable, however, from a few specimens found in the Makah Formation at LACMIP loc. 6293.

The large, low protoconch of the new species is very unusual for genus *Fulgoraria* and more closely resembles protoconchs found on some, but not all, species of the fulgorariine genera *Ericusa* H. & A. Adams, 1858, and *Livonia* Gray, 1855. In particular, the protoconchs of modern *Livonia mammilla* (Sowerby I, 1844) and *Ericusa* (*E.*) *sericata* Thornley, 1951 are very similar to the protoconch of the new species. Illustrations of these modern species, both of which are from Australia, are in Weaver & du Pont (1970:pl. 17, figs. A–C; pl. 20, figs. C–D), respectively. The new species is not assigned to either one of these genera because, according to Weaver & du Pont (1970), *Livonia* is characterized by spiral ribbing and *Ericusa* is characterized by three or more folds on the columella. In addition, the siphonal fasciole in these two genera is either indistinct or absent.

As noted by Moore (1984a), the only other described species at all similar to the new species is *Fulgoraria* (*Musashia*) *nagaoi* Shikama (1967:111–112, pl. 13, figs. 9–12) from the upper Oligocene to lower Miocene Poronai Formation, Hokkaido, northern Japan. The new species and *F. (M.) nagaoi* are unique among the fulgorarines because they have smooth shells and a well-developed siphonal fasciole. The new species differs from *F. (M.) nagaoi* in the following features: smaller size teleoconch, larger and more rounded protoconch, narrower spire, suture more inclined, and body whorl less inflated.

The new species resembles *Fulgoraria* (*Musashia*) *olutor斯基ensis* (Krishtofovich 1973:77, pl. 22, figs. 8, 9) from the Oligocene formations of northeastern Kamchatka Peninsula, Russia. The synonymy of *Fulgoraria* (*Musashia*) *olutor斯基ensis* was recently updated by Oleinik (1993). The new species differs from *F. (Musashia) olutor斯基ensis* in the following features: two columellar folds rather than one, well-developed siphonal fasciole, and an obsolete subsutural band.

The new species, along with another Washington species, *Fulgoraria* (*Musashia*) *weaveri* (Tegland, 1933:127–128, pl. 11, figs. 1–5), are the earliest undoubted records of *Musashia* in the eastern Pacific and in the world. The new species ranges from early to late Oligocene, and *F. (M.) weaveri* was reported by Addicott (1976:98) as ranging from the early through late Oligocene in the vicinity of Seattle, Washington. The new species differs from *F. (M.) weaveri* by having an almost smooth shell. We concur with Moore (1984a) that *Miopleiona scowensis* Durham (1944:177–178, pl. 17, fig. 5) from the Oligocene of Mar-

rowstone Island, Jefferson County, Washington is the same as *F. (M.) weaveri*.

There are three other reported species of *Musashia* in the eastern Pacific. One is *F. (M.) shikamai* Moore (1984a: 18, 20, figs. 49, 63, 72, 74, 75, 77, 78, 82, 83, 88, 89) from the upper part of the Lincoln Creek Formation at Knappton, Washington. This species is found in association with specimens of the new species. The age of *F. (M.) shikamai*, like that of the new species in the Knappton area, is herein tentatively assigned to the latest early Oligocene to earliest late Oligocene. The other two species of eastern Pacific *Musashia* are *F. (M.)* sp. of Allison & Marinovich (1981[1982]:pl. 3, figs. 12, 13) from the upper Oligocene or lowermost Miocene on Sitkinak Island, Gulf of Alaska; and *F. (M.)* n. sp. of Addicott (1976:pl. 4, fig. 18) from the upper Miocene of the Grays Harbor area, southwestern Washington. The new species differs from all of these other species by having an almost smooth shell.

Etymology: The new species is named in honor of Ellen James Moore for her many valuable contributions to the study of Tertiary mollusks in the eastern Pacific.

Occurrence: Early and late Oligocene (upper part of Galvinian, Matlockian, and Juanian Stages), Washington. **EARLY EARLY OLIGOCENE** (“*Echinophoria*” fax Zone): Jansen Creek Member of the Makah Formation, north side of Olympic Peninsula, Washington (herein); lower Lincoln Creek Formation, Satsop River area, Grays Harbor basin, Washington (Armentrout, 1973); **EARLY OLIGOCENE** (*Liracassis rex* Zone): Blakeley Formation, Bainbridge Island and Seattle, Washington Durham (1944). **LATEST EARLY OLIGOCENE** to **EARLIEST LATE OLIGOCENE** (approximately equivalent to the *Liracassis rex*-*Liracassis apta* Zonal boundary): Upper Makah Formation, north side of Olympic Peninsula, Washington (herein); lower part of the Pysht Formation, north side of Olympic Peninsula, Washington (herein); middle Lincoln Creek Formation, Satsop River area, Grays Harbor basin, Washington; upper Lincoln Creek Formation, Knappton area, near mouth of Columbia River (tentatively, herein). **LATE OLIGOCENE** (*Liracassis apta* Zone): Upper Lincoln Creek Formation, Satsop River area, Grays Harbor basin, Washington (Armentrout, 1973).

ACKNOWLEDGMENTS

Gail H. Goedert helped in collecting many of the specimens. Ellen J. Moore loaned specimens of the new species, provided locality information, and identified some associated fossils. Edward C. Wilson (LACMIP) allowed access to collections, provided catalog numbers, and shared his knowledge of the Knappton area. Lindsey T. Groves (Malacology Section, Natural History Museum of Los Angeles County) obtained some important references. Ross E. Berglund (Bainbridge Island) loaned a key reference. Bruce Welton (Mobil Oil Company, Dallas, Texas) iden-

tified the shark. Carole S. Hickman provided an age assignment of the strata at LACMIP loc. 6202. Hal Heitman (Unocal Corporation, Houston, Texas) processed and identified foraminifera from rocks in the Murdock Creek area. Anton E. Oleinik (Purdue University, Indiana) commented on an early version of the manuscript and kindly shared his knowledge of volutids. The manuscript benefited from reviews by Anton E. Oleinik and an anonymous referee.

Some specimens used for this report were collected during fieldwork supported by a grant (4439-90) from the National Geographic Society to the Natural History Museum of Los Angeles County Foundation for fossil cetacean research on the Olympic Peninsula.

LOCALITIES CITED

All quadrangle maps are those of the U. S. Geological Survey.

JLG 221. Mollusks collected from sandstone exposed in beach terrace, approximately 300 m SE of mouth of Jansen Creek and approximately 140 m N of SW corner of sec. 25, T. 33 N, R. 14 W, Sekiu River quadrangle, 7.5-minute, 1984 provisional edition, Clallam County, Washington. Jansen Creek Member of the Makah Formation. Age: Earliest Oligocene (Hickman, personal communication). Collectors: J. L. Goedert, 1987.

LACMIP 5842. Specimens collected at low tide from fossiliferous concretions weathering out of a landslide block in upper part of the Lincoln Creek Formation between Knappton and Grays Point, in the center of the N $\frac{1}{2}$, N $\frac{1}{2}$ of sec. 9, T. 9 N, R. 9 W, Knappton quadrangle, 7.5-minute, 1949 (photo-revised 1973), on the Columbia River, Pacific County, Washington. Upper part of the Lincoln Creek Formation. Tentative Age: Latest early Oligocene to earliest late Oligocene. Collectors: J. L. & G. H. Goedert, 1979 to date. [Locality is equivalent to USGS loc. M8995.]

LACMIP 5950. From concretions on beach and shales on beach, approximately 0.8 km (0.5 mi.) W of Shipwreck Point, and 1.1 km (0.7 mi.) E of mouth of Jansen Creek, NW $\frac{1}{4}$ of sec. 36, T. 33 N, R. 14 W, Clallam Bay quadrangle, 15-minute, 1957 edition, Clallam County, Washington. Jansen Creek Member of the Makah Formation. Age: Earliest Oligocene. Collectors: J. L. & G. H. Goedert, 1980 to 1984, and W. Buchanan, 1984.

LACMIP 6202. Invertebrate specimens collected from float and concretions weathering out of concretionary sandstone exposed on S shore of Strait of Juan de Fuca, 0.2 km W of mouth of Rasmussen Creek, NE $\frac{1}{4}$ of sec. 27, T. 33 N, R. 14 W, Clallam Bay quadrangle, 15-minute, 1957 edition, Clallam County, Washington. Jansen Creek Member of the Makah Formation. Age: Earliest Oligocene. Collectors: J. L. & G. H. Goedert, July, 1982.

LACMIP 6293. Float and *in situ* fossils from shales and

siltstones at first small point approximately 500 m W of mouth of Sekiu River, NE $\frac{1}{4}$ of sec. 8, T. 32 N, R. 13 W, Clallam Bay quadrangle, 15-minute, 1957 edition, Clallam County, Washington. Makah Formation. Age: Latest early Oligocene to earliest late Oligocene. Collectors: J. L. & G. H. Goedert, May, 1983.

LACMIP 6294. Numerous and well-preserved invertebrates exposed as small, discontinuous, concretionary lenses and masses of shells in bedrock at base of low cliff and beach terrace on S shore of Strait of Juan de Fuca, approximately 770 m W of mouth of Murdock Creek, latitude 48°09'37"N, longitude 123°52'28"W, NW $\frac{1}{4}$, NW $\frac{1}{4}$ of sec. 29, T. 31 N, R. 9 W, Disque quadrangle, 7.5-minute, 1950 (photo-revised 1978), Clallam County, Washington. Pysht Formation. Age: Latest early Oligocene to earliest late Oligocene. Collectors: J. L. & G. H. Goedert, June, 1983 to date. [Locality is equivalent to USGS loc. M8986; and float from LACMIP loc. 6294 is equivalent to USGS loc. M9002.]

LACMIP 6295. Fossils found as float (derived from rocks in the vicinity of LACMIP loc. 6294) on beach in concretions which cover the beach between 850 m and 300 m W of the mouth of Murdock Creek, NW $\frac{1}{4}$ of sec. 29, T. 31 N, R. 9 W, S shore of Strait of Juan de Fuca, Disque quadrangle, 7.5-minute, 1950 (photo-revised 1978), Clallam County, Washington. Pysht Formation. Age: Latest early Oligocene to earliest late Oligocene. Collectors: J. L. & G. H. Goedert, June, 1983 to date, April, 1984.

LACMIP 8230. Specimens collected as float on beach approximately 275 m W of point which is approximately 950 m NW of mouth of Murdock Creek, S shore of Strait of Juan de Fuca, SE $\frac{1}{4}$ of sec. 19, T. 31 N, R. 9 W, Disque quadrangle, 7.5-minute, 1950 (photo-revised 1978), Clallam County, Washington. Pysht Formation. Age: Latest early Oligocene to earliest late Oligocene. Collectors: J. L. Goedert & G. H. Goedert, 1984.

UCMP A1803. Behind Olympic Foundry, along E side of Duwamish River in southern part of Georgetown, Seattle, King County, Washington. Blakeley Formation. Age: Early Oligocene. Collector: J. W. Durham, circa early 1940s.

UCMP A1804. Conglomerate on S side of Bremerton Inlet, Middle Point, sec. 15, T. 24 N, R. 2 E, Bremerton East quadrangle, 7.5-minute, 1953 (photo-revised 1981), Kitsap County, Washington. Blakeley Formation. Age: Early Oligocene. Collector: J. W. Durham, circa early 1940s.

UCMP A1807. Conglomerate at Beans Point, SW $\frac{1}{4}$ of NW $\frac{1}{4}$ of sec. 14, T. 24 N, R. 2 E, Bremerton East quadrangle, 7.5-minute, 1953 (photo-revised 1981), Kitsap County, Washington. Blakeley Formation. Age: Early Oligocene. J. W. Durham, circa early 1940s.

UCMP A1812. Conglomerate and shale on small peninsula of S side of Bremerton Inlet, NW $\frac{1}{4}$ of SW $\frac{1}{4}$ of

- sec. 8, T. 24 N, R. 2 E, Bremerton East quadrangle, 7.5-minute, 1953 (photo-revised 1981), Kitsap County, Washington. Blakeley Formation. Age: Early Oligocene. Collector: J. W. Durham, circa early 1940s.
- UWBW B0356. Siltstone bed on S side of Middle Fork Satsop River along well exposed face, 46 m (150 ft.) along strike, 3 m (10 ft.) stratigraphic interval, 960 m (3150 ft.) W, 847 m (2780 ft.) N of SE corner of sec. 20, T. 21 N, R. 6 W, Mt. Tebo quadrangle, 15-minute, 1953 edition, Mason County, Washington. Lincoln Creek Formation. Age: Earliest Oligocene. Collectors: J. M. Armentrout & Bill Fletcher, 1971. [Locality equivalent to MF-5 of Armentrout, 1973:226].
- UWBW B0406. Siltstone, SE side of Middle Fork Satsop River, base of strata exposed along cliff face to W, 12 m (40 ft.) stratigraphically below base of sandstone exposed in cliff above, 618 m (2030 ft.) W and 1555 m (5100 ft.) N of SE corner of sec. 6, T. 20 N, R. 6 W, Mt. Tebo quadrangle, 15-minute, 1953 edition, Mason County, Washington. Lincoln Creek Formation. Age: Late Oligocene. Collectors: J. M. Armentrout and Bill Fletcher, 1971. [Locality equivalent to MF-32 of Armentrout, 1973:23].
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Identification of Monosaccharides in Hydrolyzed Bivalve Shell Insoluble Matrix

by

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Abstract. This study provides the first survey by gas chromatography/mass spectrometry of the hydrolyzed insoluble organic matrices of the following bivalve species: *Corbicula fluminea* (Müller), *Dreissena polymorpha* (Pallas), *Geukensia demissa* (Dillwyn), and *Mercenaria mercenaria* (Linnaeus). This study is important because it provides new information on a little known aspect of mollusk insoluble matrix, namely its monosaccharide composition. Six monosaccharides were identified in the form of silylated derivatives. These are altrose, fucose, galactose, glucose, mannose, and xylose. All six sugars were detected in each species in similar relative concentrations. In addition, the amino sugar galactosamine was detected in *M. mercenaria*. The monosaccharide compositions of these bivalve matrices are not only similar to each other but also are similar to results previously reported for *Nautilus pompilius* Linnaeus. The resemblance in both matrix monosaccharide identity and relative abundance of all five species suggests a possible general similarity in monosaccharide composition for mollusk insoluble matrix. While the role of these monosaccharides in the matrix is not fully determined, it is possible that some of them are constituents of glycoproteins.

INTRODUCTION

Monomeric constituents of mollusk shell organic matrix have been studied intensively for over 40 years. An important goal of this research is to describe primary structures of particular macromolecules so that structure and function of these larger molecules may be understood. Much of the information on primary structures obtained thus far has been identification and quantitation of amino acids and amino sugars present after acid-catalyzed organic matrix hydrolysis. One important outcome of this research is the identification of biomolecules that play consequential

roles in biomineralization processes (Lowenstam & Weiner, 1989).

Tevesz et al. (1992) used gas chromatography/mass spectrometry (GC/MS) to identify five monosaccharides (glucose, galactose, mannose, fucose, and xylose) not previously reported from the insoluble organic matrix of *Nautilus pompilius* Linnaeus, 1758. These compounds are <1% by weight of the organic matrix. The low concentration of monosaccharides was not indicative of a structural role for the compounds. Moreover, three of the monosaccharides (galactose, mannose, and fucose) are monosaccharide residues often found in glycoproteins. This study was dif-

Table 1
Shell and life habit characteristics of studied mollusks.

Species	Collection site	Habitat	Life habits	Shell mineralogy	Predominant microstructure
<i>Corbicula fluminea</i>	Mohegan River, Ohio	Freshwater	Shallow infaunal suspension feeder	Aragonite	Crossed lamellar, Complex crossed lamellar
<i>Dreissena polymorpha</i>	Lake Erie, Ohio	Freshwater	Epibyssate suspension feeder	Aragonite	Prismatic, Crossed lamellar, Complex crossed lamellar
<i>Geukensia demissa</i>	Beaufort, N. Carolina	Marine	Endobyssate suspension feeder	Aragonite, Calcite	Nacreous, Prismatic, Homogeneous
<i>Mercenaria mercenaria</i>	Commercial Supplier	Marine	Shallow infaunal suspension feeder	Aragonite	Prismatic, Crossed lamellar, Complex crossed lamellar
<i>Nautilus pompilius</i>	Commercial Supplier	Marine	Nektonic predator	Aragonite	Nacreous, Prismatic

ferent from previous studies because it surveyed matrix for monomeric constituents of polysaccharides instead of amino acids and amino sugars.

In the present study, we used GC/MS in order to survey the insoluble matrix of four species of bivalve mollusks for monosaccharides. This study is important because it presents new descriptive information on the monosaccharide composition of mollusk matrix. We also compared the results obtained from this study with the results obtained for *Nautilus pompilius*. If different sugars in varying relative abundances are found comparing the bivalves as a group to *N. pompilius*, then this would suggest a possible relationship between carbohydrate composition and factors such as taxonomy, ecology, and shell microstructure, because the bivalves and cephalopod are different from each other in these ways. If, on the other hand, similar sugars are found, then this result could suggest a possible general similarity in monosaccharide composition for mollusk insoluble matrix.

MATERIALS AND METHODS

The materials analyzed in this study are the insoluble organic matrices of four species of bivalve mollusks collected alive: *Corbicula fluminea* (Müller, 1774), *Dreissena polymorpha* (Pallas, 1771), *Geukensia demissa* (Dillwyn, 1817), and *Mercenaria mercenaria* (Linnaeus, 1758). Information on their taxonomy, collection sites, habitat, life habits, shell mineralogy and microstructure is presented in Table 1, along with comparative data on *Nautilus pompilius*.

Sample preparation and analysis procedures are the same as those described in detail in Tevesz et al. (1992). Briefly, insoluble matrix was obtained from all four bivalve species in the following way: Cleaned whole shells were fragmented, brushed, soaked in Clorox, washed in distilled water, dried, and ground into powder. The powder was

decalcified using the di-sodium salt of ethylenediaminetetraacetic acid (EDTA) dissolved in water and stirred. The resulting EDTA solution and suspended material (insoluble matrix fragments) were centrifuged until the matrix was condensed into a pellet in the bottom of the centrifuge tube. This pellet was repeatedly washed with distilled water and then dried in a vacuum desiccator. Sodium azide was used during the process as an antibacterial agent.

Insoluble matrix was prepared for analysis by GC/MS by hydrolysis in 4N trifluoroacetic acid. The residue from this hydrolysis was heated in a mixture of pyridine and bis(trimethylsilyl)trifluoroacetamide (BSTFA) containing a known amount of mannitol as an internal standard. Treatment with BSTFA created trimethylsilylated derivatives of matrix compounds and allowed for their analysis by GC/MS.

The derivatized compounds present in the hydrolyzed matrix were analyzed and quantified by GC/MS using a Finnegan TSQ 45 mass spectrometer. Compound identification was performed by comparison of both mass spectra and retention times to those obtained from authentic samples. Quantification was accomplished by comparing peak areas from the matrix sample with those from the standard solution, and then comparing these peaks to those of the internal standard in light of appropriate response factors.

RESULTS

Six monosaccharides (glucose, mannose, galactose, altrose, fucose, and xylose) were identified in the form of silylated derivatives in matrix samples after hydrolysis and are listed and quantified in Table 2. All six monosaccharides were found in each species in similar relative abundances. Glucose and mannose are the two most abundant compounds, followed by galactose and altrose. Xylose and fucose are

Table 2
Sugar analysis: Monosaccharides in hydrolyzed mollusk shell insoluble matrix, by gas chromatography/mass spectrometry.

Species	Compound											
	Glucose			Mannose			Galactose			Altrose		
	W%	M%	T%	W%	M%	T%	W%	M%	T%	W%	M%	T%
<i>Corbicula fluminea</i>	57.0	56.7	0.02	24.4	24.3	0.01	7.0	7.0	<0.01	9.6	9.6	<0.01
<i>Dreissena polymorpha</i>	55.7	55.8	0.07	17.9	17.9	0.02	6.1	6.1	0.01	13.0	13.0	0.01
<i>Geukensia demissa</i>	36.0	35.8	0.03	43.5	43.2	0.03	12.2	12.1	0.01	5.3	5.3	<0.01
<i>Mercenaria mercenaria</i>	55.6	55.3	0.09	28.7	28.6	0.04	6.7	6.7	0.01	6.7	6.7	0.01
<i>Nautilus pompilius</i> *	51.7	50.8	0.22	25.3	24.9	0.11	12.8	12.6	0.05	ND	ND	0.03

* Data from Tevesz et al. (1992); W% = weight %; M% = mole %; T% = weight % of total sample; ND = not detected.

Table 3

Comparison of *N. pompilius* monosaccharide composition with bivalve mean composition (composition numbers are in mole percent).

	Glucose	Man-nose	Galac-tose	Xylose	Fucose
<i>N. pompilius</i>	50.8	24.9	12.6	7.3	4.5
Bivalve mean	50.9	28.5	8.0	2.7	1.3
Bivalve standard error of mean	5.0	5.4	1.4	0.7	0.4
F-ratio (d.f. = 3,1)	0.0004	0.449	11.108	38.269	54.306
P value*	0.99	0.55	0.04	0.009	0.005
Multivariate F-ratio† (d.f. = 3,1)	84.9465, $P = 0.0796$				

* Critical value for significance is $P = 0.05/5 = 0.01$.

† Wilks' Lambda F-test of the hypothesis that the bivalve mean of (glucose, mannose, galactose) is equal to the *N. pompilius* multivariate point (50.8, 24.9, 12.6). $P = 0.05$ is used as the critical value for significance.

the least abundant compounds in all four species. Overall, the carbohydrate material present in the matrices of these species is small (<1%).

In addition to these detected monosaccharides, the following ones were also derivatized with BSTFA and analyzed as standards: arabinose, lyxose, rhamnose, ribose, and talose. Derivatives of these sugars were detected by GC/MS in standards but not in matrix samples of the four bivalve species. Thus, it is unlikely that they are present in the insoluble matrices in detectable levels. Galactosamine was detected in the *M. mercenaria* samples. Although the hydrolysis and derivatization procedures used in this study have proven successful for consistently detecting and quantifying most monosaccharides, they were not successful for glucosamine (Tevesz et al., 1992). Therefore, we do not report quantitations for this compound.

A statistical comparison of bivalve mean monosaccharide composition (expressed as mole %) with *N. pompilius* composition is presented in Table 3.

DISCUSSION

The monosaccharide compositions of the bivalves are similar to each other as evidenced by the relatively small standard errors, at least for those sugars that compose most of the insoluble matrix (glucose, mannose, galactose; Table 3). Bivalve sugar composition can be compared to *N. pompilius* composition in two ways. In the first, the mean sugar mole percents of the four bivalve species are compared to the corresponding *N. pompilius* value. In other words, the null hypothesis is $\beta_i = n_i$, where β_i is the means of the five monosaccharides for which there are comparable data, and n_i is corresponding *N. pompilius* sugar mole percents. A Bonferroni adjustment procedure was used to control the overall comparison error rate. If the overall comparison level for the five comparisons is to be 0.05, then the P value

0.01 ($=0.05/5$) must be used for any single hypothesis test. Table 3 indicates that the bivalves are similar to *N. pompilius* (the null hypothesis is not rejected) for glucose, mannose, and galactose. Because these sugar percents appear to be highly correlated with one another, a more appropriate test of similarity would be to compare the multivariate bivalve mean to the *N. pompilius* multivariate value. Unfortunately, there are not enough data for a test of all five sugars. However, a test of the three most abundant sugars shows that the monosaccharide composition of the bivalves is similar to *N. pompilius* (Table 3).

The similarity in matrix carbohydrate composition between the bivalves and *N. pompilius* suggests that this aspect of matrix chemistry is not correlative with taxonomical, ecological, or microstructural differences. The bivalves as a group are different from *N. pompilius* in these respects (e.g., ordinal classification, life habits, kinds of microstructures; Table 1) yet they are statistically similar in terms of the nature and quantity of the most abundant monosaccharides.

In addition, the resemblance in both matrix monosaccharide identity and relative abundance of all five species possibly suggests the existence of a monosaccharide common chemistry for mollusk insoluble matrix. This consistency of composition shows parallels with reported amino acid and amino sugar compositions. One or two amino acids are dominant in most insoluble matrices. These abundant amino acids are glycine or glycine and alanine (Meenakshi et al., 1971; Grégoire, 1972). These monomers are believed to be building blocks of hydrophobic proteins. The amino sugar glucosamine also occurs abundantly in the insoluble fraction of many species. It is the monomeric constituent of chitin in its β -form which is located between protein sheets (Goffinet & Jeuniaux, 1969; Weiner & Traub, 1980).

The function of monosaccharides detected in the insoluble matrix is not fully known. Tevesz et al. (1992) reported three monosaccharides found in *N. pompilius* matrix (galactose, mannose, and fucose) which are important monosaccharide constituents of glycoproteins (Montgomery, 1970). Montgomery (1970) also reports that the amino sugars glucosamine and galactosamine are important carbohydrate constituents of glycoproteins. In 1992, we reported finding glucosamine in *N. pompilius* insoluble matrix after hydrolyzing the samples in HCl, confirming the findings of several other workers. In this study, we detected

galactosamine in the matrix of *M. mercenaria*. Taken together, the presence of galactose, mannose, and fucose in all analyzed matrices, plus the presence of glucosamine and galactosamine in some of the species, suggests the possibility of a pervasive presence of glycoproteins in mollusk insoluble matrix.

Sulfated glycoproteins are already known to compose a major portion of the EDTA soluble portion of mollusk matrix (Simkiss, 1965; Crenshaw, 1972). These proteins are rich in aspartic acid and can bind calcium ions. In light of these findings, our results suggest the importance of glycoproteins to the matrix as a whole. Nevertheless, the low concentration of monosaccharides (<1%) is not indicative of a structural role for the compounds in the insoluble matrix.

ACKNOWLEDGMENTS

The authors thank the Lewis Research Center (NASA) for the donation of the mass spectrometer used in this work.

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Evolution of Labral Spines in *Acanthais*, New Genus, and Other Rapanine Muricid Gastropods

by

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Abstract. The new genus *Acanthais* is proposed for *Acanthina brevidentata* (Wood, 1828), a rapanine muricid gastropod common on tropical eastern Pacific rocky shores. It is distinguished by the presence of a labral spine, a central fold on the columella, and other characters of the shell and radula. *Acanthais* is one of at least five members of the Rapaninae in which a labral spine has evolved independently. This feature is an exaggeration of an enlarged ventrally projecting crenation at the base of the outer lip. Such crenations are widespread in the Rapaninae. Biogeographically, *Acanthais* is one of at least eight endemic tropical eastern Pacific genera of gastropods with an origin during or after the Pliocene.

INTRODUCTION

Acanthina brevidentata (Wood, 1828) is a common intertidal muricid gastropod in the tropical eastern Pacific (Keen, 1971), belonging to the Rapaninae (Thaidinae of authors; see Kool, 1993b). Because of the presence of a labral spine (a ventrally projecting spine near the base of the outer lip), the species has usually been assigned to the ocenebrine muricid genus *Acanthina*. Cooke (1918), Wu (1985), and Vermeij (1993) realized that this assignment is incorrect, but did not provide a more suitable taxonomic placement. Here we erect the new genus *Acanthais* to accommodate the species. We also take the opportunity to comment on the evolution of labral spines among Rapaninae and on the biogeographical distinctness of a number of rocky-shore gastropod genera in the tropical eastern Pacific.

MATERIALS AND METHODS

All specimens used in the analysis of teleoconch characters are housed in the Vermeij collection. Fifteen lots of *Acanthina brevidentata* spanning a geographical range from northwestern Costa Rica to southern Ecuador were examined. Characters of shell microstructure, operculum, radula, and anatomy were assessed in six male and six female specimens of *A. brevidentata* from Venado Island,

Panama (MCZ Number 298408). J. H. McLean of the Los Angeles County Museum kindly supplied us with specimens on which the protoconch was preserved (LACM 70-65.29, Playa del Coco, Costa Rica). For methods of dissecting protocol and preparation for SEM photography of the radula, protoconch, and shell microstructure, see Kool (1993b).

Throughout the text, generic names are used in the narrow sense unless otherwise indicated, and the names of type species are those currently accepted rather than the names originally designated.

SYSTEMATICS

Family MURICIDAE Rafinesque, 1815

Subfamily RAPANINAE Gray, 1853

Genus *Acanthais* Vermeij & Kool, gen. nov.

Type species: *Acanthais brevidentata* (Wood, 1828).

Diagnosis: Rapanine with a teleoconch sculpture of spiral cords, up to five on body whorl, bearing low rounded nodes, the two adapical cords often obsolete or missing; secondary sculpture of exceedingly fine spiral threads; outer lip bearing short labral spine adapical to fifth major spiral cord;

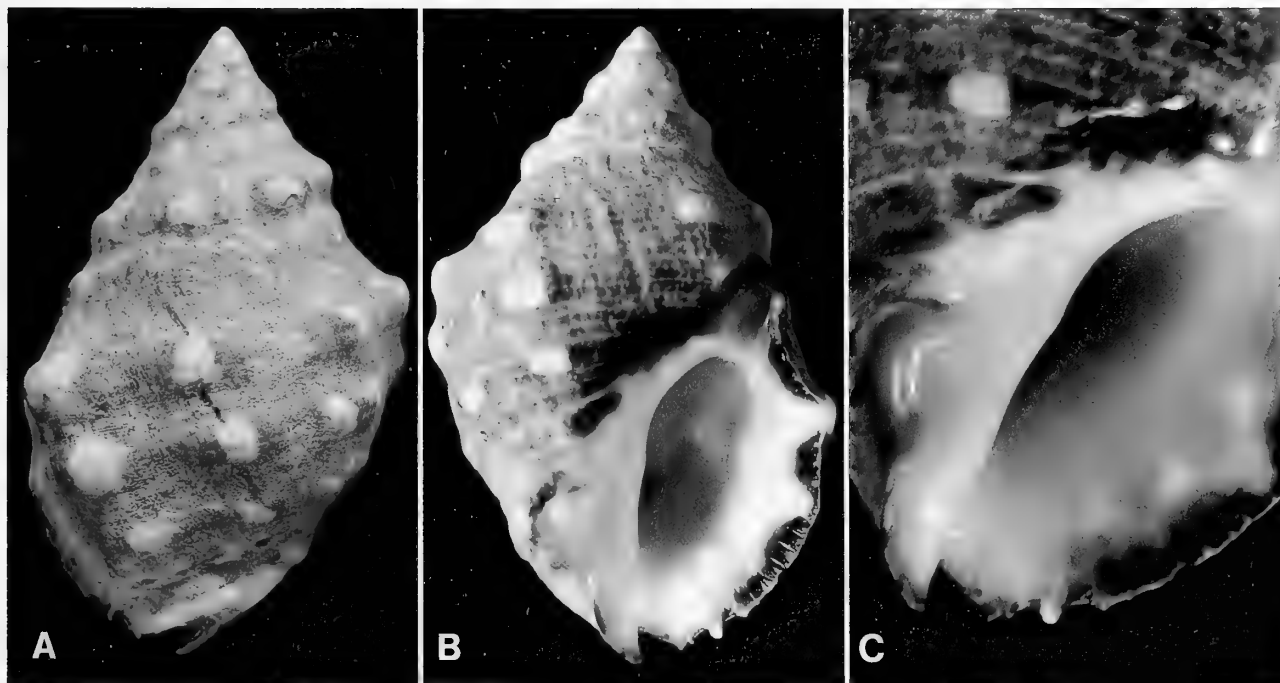


Figure 1

Shell morphology, *Acanthais brevidentata* Vermeij & Kool, gen. nov., Isla Taboga, Panama, collected 25 February 1986. A. dorsal view, $\times 3$. B. apertural view, $\times 3$. C. basal portion of outer lip, $\times 3$.

inner surface of outer lip denticulate, without lirae; columella straight, bearing distinct central fold that extends into aperture.

Acanthais brevidentata (Wood, 1828)

(Figure 1)

Buccinum brevidentatum Wood, 1828:12.

Monoceros brevidentata Wood, 1828:43.

Description: *Protoconch*. Moderately tall, of about 3.5 adpressed whorls (exact count could not be made from available specimen), and with well-developed outward-flaring lip and sinusigeral notch (Figure 2). Angular, ridged shoulder on last 1.5 whorls. Series of vertical plicae on area close to end of last whorl. Subsutural plicae on last 2.5 whorls. Increasingly well developed ridged shoulder with subsutural plicae. Last whorl with small pustules and with vertical plicae on last quarter whorl.

Shell Morphology. Shell moderately high-spined (apical half-angle of spire 30° to 36°), sutures between teleoconch whorls distinct; umbilical slit absent; siphonal canal short, broad, forming upturned notch at basal end, and set off from remainder of last whorl by prominent fasciole. Teleoconch whorls sculptured by major nodose spiral cords and by numerous exceedingly fine spiral threads; on last whorl up to five primary cords, one at the suture, two central

ones with prominent low rounded nodes, and two subordinate basal cords of which one (the most basal cord) is often missing. Outer lip crenate at edge, bearing short, sharp labral spine at position basal to abapical (fifth) primary spiral cord and situated at the end of a shallow external groove. Inner edge of outer lip with four weakly elongate denticles situated close to the edge of the lip; inner surface of outer lip otherwise smooth, not lirate. Apical end of aperture constructed by prominent parietal rib; no anal slit. Columella straight, with more or less distinct central fold extending into the aperture and one or more weak basal riblets that are confined to the ventral surface of the inner lip.

Shell Microstructure. Inner layer of aragonite with crystals oriented in a 45° -degree angle to the growing edge (Figure 3A); middle layer of aragonite with crystals oriented perpendicular to growing edge; outer layer of aragonite with crystal planes oriented parallel to growing edge. Inner layer absent in some specimens.

Operculum. D-shaped, but upper end more rounded, with lateral nucleus in center right. Free surface with bracket-shaped growth lines; attached surface with 3–4 bracket-shaped growth lines and with callused, glazed rim (about 30–35% of opercular width) on left.

Anatomy. The anatomy of *Acanthais brevidentata* is typically rapanine, and schematic drawings of anatomical features, as well as detailed explanations of terminology used,

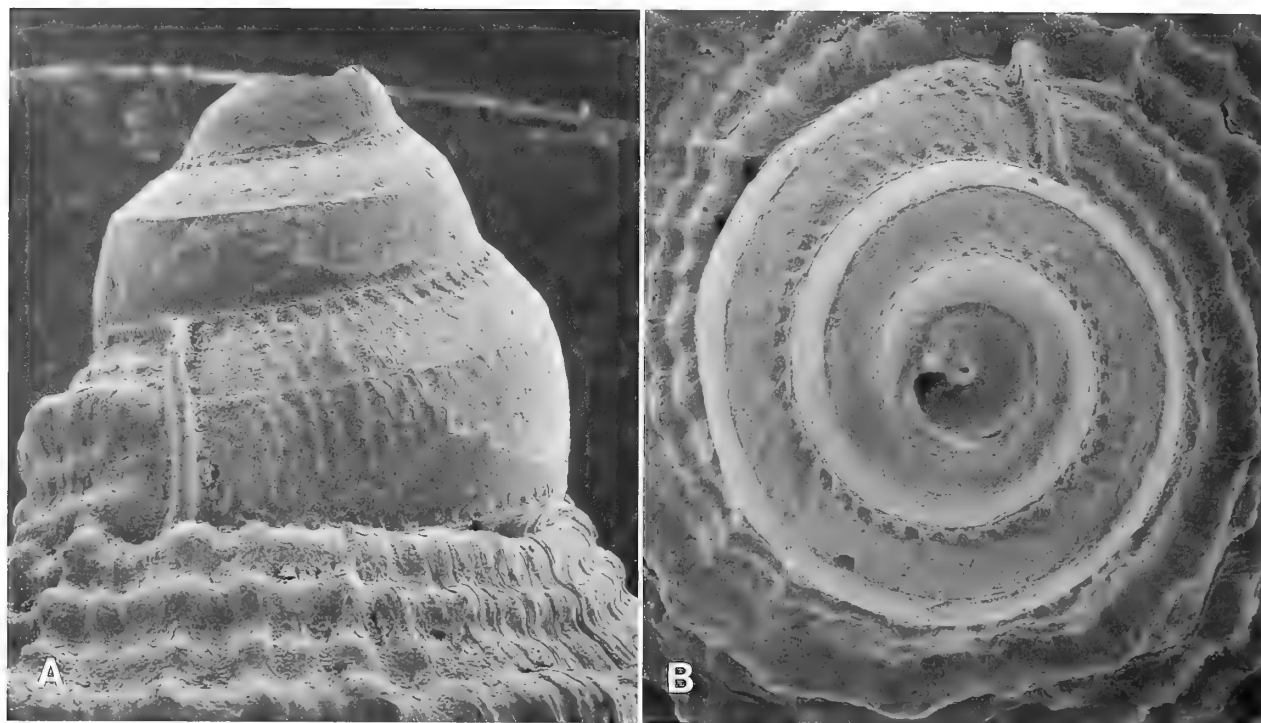


Figure 2

Protoconch, *Acanthais brevidentata* Vermeij & Kool, gen. nov., Playa del Coco, Costa Rica, LACM 70-65.29. A. lateral view, $\times 80$. B. apical view, $\times 80$.

can be found in previous papers by Kool (1989, 1993a, b). It should be noted that coloration given for the anatomical features described below is found in the living animals and may have faded or disappeared following preservation in alcohol.

Head and foot. Foot flecked with grey, black, and orange; edge primarily orange with minute white specks; sole opaque grey. Cephalic tentacles elongate, thin, dark brown with grey tips. Incurrent siphon with white and orange specks proximally, flecked with black distally. Accessory boring organ elongate, well developed; in females dorsal to short ventral pedal gland.

Mantle cavity. Osphradium about two-thirds of ctenidial length, equal in width to ctenidium. Right pecten wider than left. Each lamella (12–15/mm) attached to mantle roof along one-half its length. Anteriormost portion of ctenidium curving around anterior osphradium. Ctenidial lamellae (14–17/mm) with strongly convex lateral edges, more wide than high anteriorly, more high than wide posteriorly. Supporting rods extending beyond lateral edge of each lamella, forming small papilla.

Female reproductive system. Vaginal opening inconspicuous, starting with small fold onto rectum, continuing as minute duct without obvious area for sperm storage. Small, looped flange creating ventral channel, located under small ventral lobe anteriorly, in lower center between

left and right lobes posteriorly. Ventral lobe small anteriorly, increasing in size toward posterior, until disappearing completely posteriorly. Ingesting gland dark green to black, partially located on left side of posterior capsule gland and albumen gland, extending to kidney. Ingesting gland consisting of many smaller compartments filled with dark brown material. Albumen gland omega-shaped with several posterior seminal receptacles on dorsal side entering into gland (see Kool, 1988). Albumen gland anteriorly opening into ovi-sperm duct, posteriorly into oviduct. Ovary golden yellow. Minute, papillalike pseudopenis present in most females examined.

Male reproductive system. Penis small (slightly larger than tentacle), sinuous, flattened dorso-ventrally, elliptical in cross-section, gradually tapering, almost transparent, grey opaque. Penial vas deferens a duct-within-a-duct (Kool, 1988:fig. 3B), located toward anterior and dorsally. Cephalic vas deferens minute, poorly developed. Prostate gland orange-golden from outside, with spongy texture and with one or two poorly developed ducts. Posterior vas deferens well developed, dark brown.

Alimentary system. Paired accessory salivary glands thin, short (one-ninth shell height); left gland adjacent to left salivary gland; right gland loose from right salivary gland. Salivary glands overlying short, pear-shaped valve of Leiblein. Salivary ducts attached to esophagus directly ante-

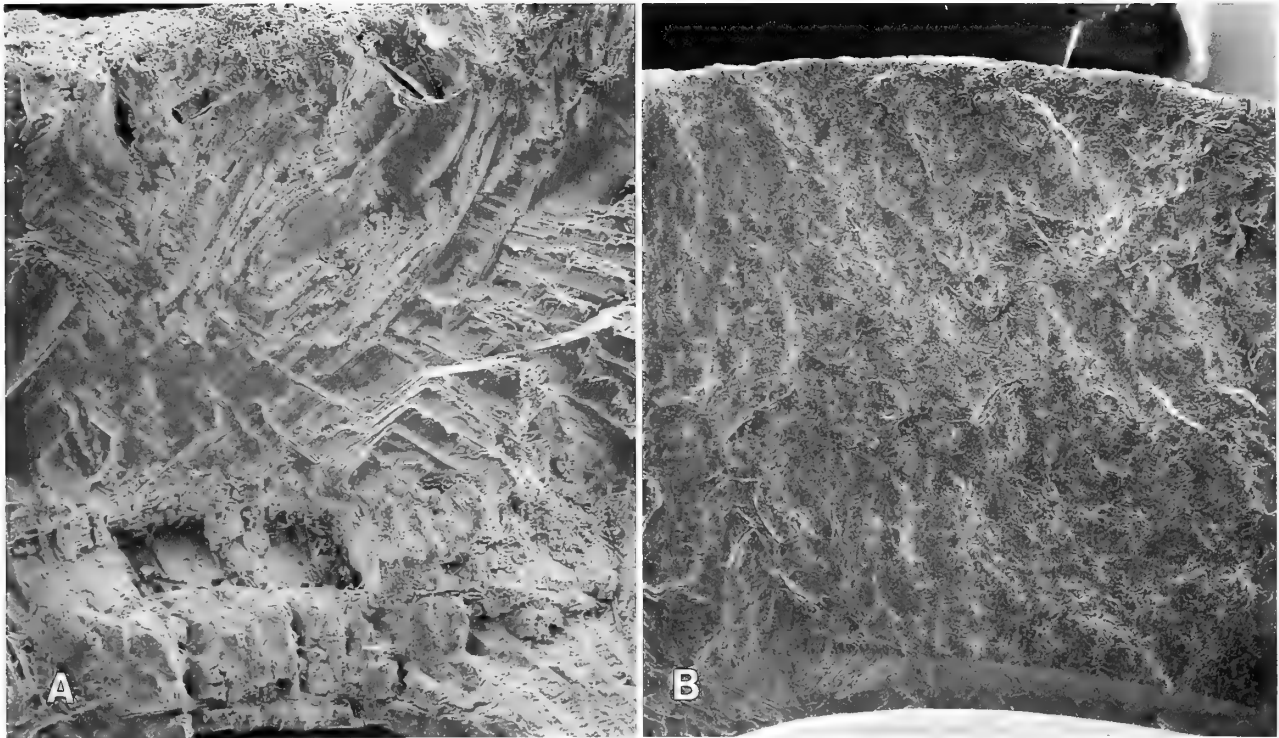


Figure 3

Shell microstructure. A. *Acanthais brevidentata* Vermeij & Kool, gen. nov., Venado Island, Panama, MCZ 298408, $\times 50$. B. *Acanthina unicornis*, Talcahuano, Chile, MCZ 3717, $\times 30$.

rior to valve of Leiblein. Glandular folds in mid-esophageal region not visible. Connection between mid-esophagus and gland of Leiblein poorly developed, very short. Posterior esophagus attached to gland of Leiblein by connective tissue. Gland of Leiblein with thick strawlike membrane obscuring spiral nature of gland. Posterior duct longer than one-half length of gland of Leiblein, emptying into dorsal branch of the afferent renal vein. Stomach a widened tube, with many small folds on posterior mixing area, oriented toward center. Stomach typhlosole and intestinal typhlosole well developed. Two digestive diverticula present. Digestive gland dark yellow to light brown. Rectal gland wide, dark green, along two-thirds of capsule gland in females, along three-fourths of prostate gland in males.

Radula. Ribbon length 30–35% of shell height. Central cusp of rachidian wide, flame-shaped; inner lateral denticle low on base of lateral cusp; outer edge of lateral cusp with one denticle (in some specimens only a remnant); marginal area with two marginal denticles and well-developed marginal denticle (Figure 4A). Lateral teeth nearly equal to width of rachidian tooth (Figure 4B).

Comparative remarks: *Protoconch.* The protoconch is typically rapanine; it is multispiral with 3+ whorls (exact figure cannot be given due to imperfect preservation of

protoconch specimen) as opposed to the typical paucispiral protoconch in ocenebrines of 1.5 whorls; and the outward-flaring lip and sinusigeral notch are indicative of a planktotrophic larval stage, found in all rapanines and absent in ocenebrines. The *Acanthais* protoconch is similar to that of *Stramonita* in both overall shape and sculptural pattern.

Shell Morphology. *Acanthais* bears a strong superficial resemblance to three ocenebrine genera, *Acanthina* Fischer von Waldheim, 1807 (type species: *A. monodon* (Pallas, 1774), southern South America); *Acanthinucella* Cooke, 1918 (type species: *A. punctulata* (Sowerby, 1835), California); and *Spinucella* Vermeij, 1993 (type species: *S. tetragona* (Sowerby, 1825), Pliocene, North Sea Basin). All four genera possess a labral spine and strong spiral cords. *Acanthais* differs from members of the Ocenebrinae by columellar, apertural, and sculptural characters.

Like many Rapaninae, *Acanthais* has sculpture on the columella. In *Acanthais*, there is a central fold. This fold is much weaker than the central fold of *Cymia* Mörch, 1860 (type species: *C. tecta* (Wood, 1828), tropical eastern Pacific). The latter genus differs widely from *Acanthais* in its lirated aperture, fine spiral ribs, adapical apertural notch, and strong peripheral tubercles. Ocenebrines have a smooth columella. Some rapanines also have a smooth

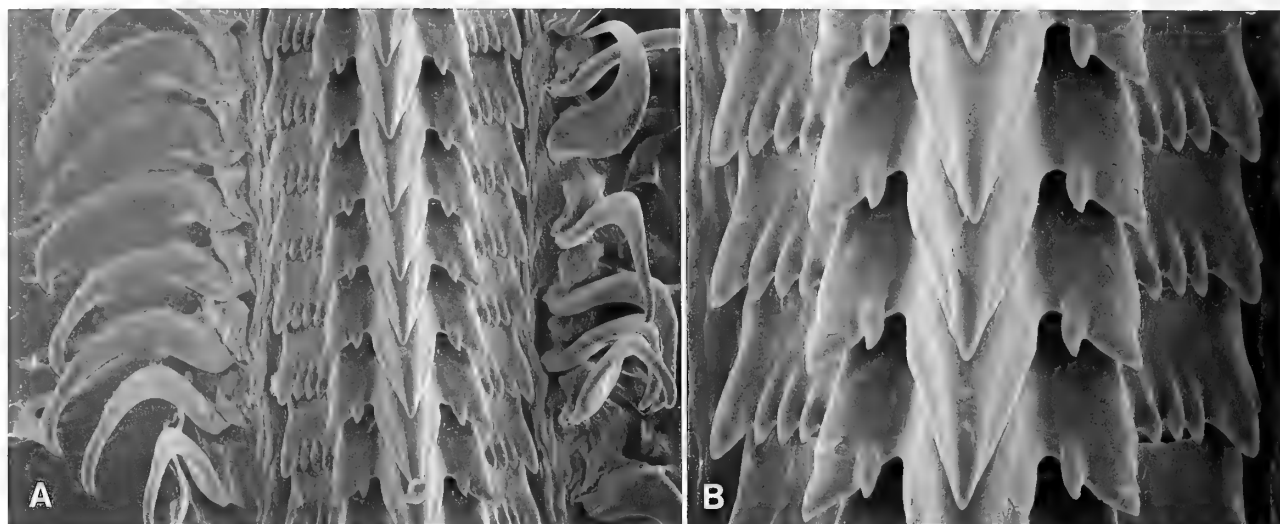


Figure 4

Radula, *Acanthais brevidentata* Vermeij & Kool, gen. nov., Playa del Coco, Costa Rica, LACM 70-65.29. A. $\times 450$. B. rachidian tooth, $\times 1000$.

columella. These include *Concholepas* Lamarck, 1801 (type species: *C. concholepas* (Bruguère, 1789), western South America); *Rapana* Schumacher, 1817 (type species: *R. bezoar* (Linnaeus, 1758), Indo-Pacific); *Ecphora* Conrad, 1843 (type species: *E. quadricostata* (Say, 1824), Pliocene of Virginia); and limpetlike morphs of *Plicopurpura* Cossmann, 1903 (type species: *P. columellaris* (Lamarck, 1816), tropical eastern Pacific). These taxa are low-spired to limpetlike, and have a sculptural pattern different from that of *Acanthais* and related genera.

In *Acanthais*, there is a parietal rib that terminates as a distinct knob at the apical end of the aperture. This feature is absent in most Ocenebrinae, including *Acanthina* and *Spinucella*. Some species of *Acanthinucella* and many populations of *Nucella emarginata* (Deshayes, 1839) from California possess a parietal tubercle, but this feature is discrete and is not a spiral parietal rib as it is in *Acanthais* and most other Rapaninae. A similar parietal rib occurs in members of Muricinae.

The five-rib pattern of major spiral cords on the body whorl sets *Acanthais* apart from Ocenebrinae but links it to many members of the Rapaninae. The adapical cord, or subsutural ridge, lies just below the suture and periodically forms apically directed extensions that produce weak knobs. At the outer lip, the most recently formed of these extensions produces a gutterlike extension with the opposing terminus of the parietal rib. The subsutural cord and corresponding posterior apertural gutter are found in nearly all Rapaninae but are lacking in *Acanthina*, *Acanthinucella*, *Spinucella*, and other Ocenebrinae. Most ocenebrines have seven or more primary spiral cords. Mem-

bers of the *Acanthinucella lugubris* (Sowerby, 1821) group from northwest Mexico (see Wu, 1985) have only four primary spiral cords, the two apical ones bearing nodes and the two basal cords being broadly rounded and set close together. Recent specimens of the *Nucella emarginata* species complex have five major cords, but there is no subsutural cord as in Rapaninae.

Among rapanine genera, *Acanthais* bears a strong superficial resemblance to *Stramonita* Schumacher, 1817 (type species: *S. haemastoma* (Linnaeus, 1767), Mediterranean and West Africa). In both genera, cords 2 and 3 on the body whorl (counting from the suture) are adorned with a row of equally prominent nodes. The primary cords of *Stramonita*, however, are narrow and angular, whereas those of *Acanthais* are low, broad, and round-topped. Moreover, the two genera differ in secondary spiral sculpture and in the way that the primary cords are reduced in many populations. In *Acanthais*, cord 5 (the most basal one) is rarely expressed, so that the primary sculpture appears to consist of three closely spaced cords on the central portion of the body whorl and a very weak noded subsutural cord. The entire shell surface is overlain by extremely fine spiral threads. In populations of *Stramonita* in which the primary spiral cords are reduced, the primary cords are of the same size as, and are difficult to distinguish from, the relatively coarse secondary cords or riblets. This is especially so in western Atlantic populations of *S. haemastoma* (belonging to the subspecies *floridana* Conrad, 1837, and *canaliculata* Gray, 1839), in the eastern Pacific *S. biserialis* (Blainville, 1832; Figure 1D-F), and in the Peruvian *S. delessertiana* (Orbigny, 1941). These typical

species of *Stramonita* also differ from *Acanthais* by the presence of riblets (lirae) on the inner side of the outer lip. Lirae are absent in *Acanthais*. Moreover, typical species of *Stramonita* lack the central columellar fold of *Acanthais*, and also lack a labral spine.

The tropical eastern Pacific genus *Neorapana* Cooke, 1918 (type species: *N. muricata* (Broderip, 1832)) resembles *Acanthais* in possessing a short labral spine in a position just basal to cord 5. In shell characters, *Neorapana* differs from *Acanthais* by lacking the central columellar fold, by having the inner side of the outer lip lirate rather than smooth, and by possessing an umbilical slit.

Several Indo-West-Pacific rapanines are also superficially similar to *Acanthais*. *Thais aculeata* (Deshayes & Milne Edwards, 1844) is the type of *Thalessa* H. & A. Adams, 1853, but was assigned to *Stramonita* by Fujioka (1985) on the basis of radular characters and to *Mancinella* Link, 1807 (type species: *M. alouina* (Röding, 1798), tropical Indo-Pacific) by Tröndle & Houart (1992). This species and its relatives have a weak to obsolete central columellar fold and, like *Acanthais*, a nonlirate outer lip bearing denticles on its inner side. However, whereas it is the fifth (most basal) primary spiral cord that is often missing in *Acanthais*, the fourth cord is usually weakest in the *T. aculeata* group. Strong erect spines adorn all five cords or all but the fourth cord in *Thalessa*. The coarse secondary spiral sculpture of *Thalessa* resembles that of *Stramonita* rather than the fine threads of *Mancinella* or *Acanthais*. It may be that *Thalessa* is close to *Stramonita*, but further anatomical study is needed to clarify the placement of this group.

Finally, *Acanthais* shares many features with *Thais* Röding, 1798 (type species: *T. nodosa* (Linnaeus, 1758), tropical West Africa). Species of *Thais* resemble *Acanthais* in having exceedingly fine secondary spiral sculpture and in lacking lirae on the inner side of the outer lip, but they lack a central columellar fold and a labral spine. In *T. nodosa*, all five primary spiral cords are usually well developed and bear nodes or tubercles; but in the closely similar *T. meretricula* Röding, 1798, from the central Atlantic islands, the shell surface is covered by very fine spiral sculpture and lacks distinct primary cords. Three tropical American species, the Atlantic *T. deltoidea* (Lamarck, 1822) and the eastern Pacific *T. speciosa* (Valenciennes, 1832) and *T. triangularis* (Blainville, 1832), compose a group in which the fourth primary spiral cord is obsolete or absent. Cords 2, 3, and 5 are adorned with tubercles or nodes. In *Acanthais*, the fifth cord is obsolete or absent, and cords 2 and 3 are adorned with blunt low nodes.

A summary of the distribution of shell-character states in some rapanine general is presented in Table 1. We believe that the combination of traits clearly marks *Acanthais brevidentata* as a rapanine, but sets it apart from the previously named higher taxa in that subfamily.

Shell Microstructure. The shell microstructure shows close

phylogenetic ties with some New World rapanine genera such as *Pliocypura* and *Vasula*, both of which appear to have the three aragonitic layers and to lack calcite. This structure differs from that of *Acanthina* and other *Ocenebrinae*. *Acanthina unicornis* has one aragonitic layer with a thick calcitic layer (Figure 3B), like that found in most specimens of other *ocenebrines* (*Nucella*, *Forreria*) and *trophonines* (*Trophon*). A double layer of aragonite, as found in some specimens of the latter three genera (Kool, 1993a), was not seen in *Acanthina unicornis*. A single layer of aragonite and a thick layer of calcite also occur in a few "primitive" rapanines, such as *Stramonita*, *Concholepas*, and *Dicathais* (Kool, 1993b).

Operculum. The operculum is similar to that of *Thais*; it is D-shaped and has a lateral nucleus in the center right. In *ocenebrine* genera, the nucleus lies below the center right to the lower right.

Anatomy. The female and male reproductive systems of *Acanthais brevidentata* are very similar to those of, for example, *Thais* and *Rapana*. *Acanthais* lacks a sacklike anterior bursa copulatrix as is present in *Acanthina*, *Nucella*, and *Ocenebra*; furthermore, it has posterior seminal receptacles at the dorsal periphery of the albumen gland, which are absent in *ocenebrines*; and the accessory boring organ and ventral pedal gland share a common duct to the outside, whereas *ocenebrines* have a separate duct for both the ventral pedal gland and the accessory boring organ.

In males of *Acanthais* the prostate is closed, whereas in *ocenebrines* it is open to the mantle cavity posteriorly, and the penis is typically rapanine: sinuous with a vas deferens of the duct-within-a-duct system (Kool, 1988, 1989, 1993a, b).

The accessory salivary glands in *Acanthais* are very short relative to the shell height, whereas *ocenebrines*, such as *Acanthina*, have glands measuring about one-half the shell height. The gland of Leiblein in *Acanthais* is covered by a membrane of interwoven strings of connective tissue; such a membrane is absent in *ocenebrines*. The posterior blind duct of the gland of Leiblein is long (at least one-half of gland length) and opens into the dorsal branch of the afferent renal vein; this duct is very short (less than one-fourth of gland length) in *ocenebrines* and does not reach beyond the posterior buccal cavity.

Radula. The radula of *Acanthais brevidentata* (Figure 4) differs from that of *Acanthina unicornis* (Figure 5) and *Acanthinucella angelica* (Figure 6) in the following ways. The rachidian of *Acanthais* has a wide marginal area with three well-developed marginal denticles and marginal cusp, much as in, for example, *Purpura* and *Drupa* (Kool, 1993b). The rachidian of *Acanthina unicornis* lacks a marginal area, and the base of the serrated outer edge of the lateral cusp connects with the base of a large marginal cusp. Furthermore, it has the bifid edge typical in such genera as *Nucella* and *Ocenebra*, but differs from these in having the central cusp oriented in the same plane as the lateral cusps, rather

Table 1
Distribution of shell-character states among some genera in the Rapaninae.

Character and Character State	Ac	Co	Cy	Ma	Me	Ne	Pl	St	Th	Tl
Central columellar fold										
Present	+		+				⁺ ¹			+
Absent		+		+	+	+	⁺ ¹	+	+	
Primary cords on body whorl										
More than 10		+	+							
6 to 7							+			
5	+			+	+	+		+	+	+
Position of cords obsolete on last whorl										
All cords								⁺ ¹	⁺ ¹	
Fourth rib									⁺ ¹	+
First and fifth ribs					+					
Fourth and fifth ribs	+									
None		+		+		+	+	⁺ ¹	⁺ ¹	+
Secondary spiral sculpture										
Coarse		+	+				+	+		
Fine to very fine	+			+	+	+			+	+
Adapical notch										
Present			+				+	⁺ ²		
Absent	+	+		+	+	+		⁺ ²	+	+
Umbilical slit										
Present						+				
Absent	+	+	+	+	+		+	+	+	+
Liration on outer lip										
Present			+	+	+	+		+		
Absent	+	+					+		+	+
Nodes on spiral cords										
Pointed		+	+	+	+	+	+	+	+	+
Rounded	+									
Absent									⁺ ¹	
Labral spine										
Basal to all cords		+								
Basal to fifth cord	+					+				
Basal to fourth cord				+						
Absent			+		+		+	+	+	+

Key: Ac *Acanthais*; Co *Concholepas*; Cy *Cymia*; Ma *Mancinella*; Me *Menathais*; Pl *Plicopurpura*; St *Stramonita*; Th *Thais*; Tl *Thalessa*.
+ indicates all member have the character state in question; ¹ indicates that some individuals have the character state in question; ² indicates that members of *Stramonita* s.s. lack, whereas species of the subgenus *Thaisella* Clench, 1947, possess an adapical notch.

than it leaning backward (see Kool, 1993a). The rachidian of *Acanthinucella angelica* bears well-developed outer denticles on a more gently sloping lateral cusp, and has a bifid edge. The radula of *Acanthais* most closely resembles that of *Tribulus planospira* (see Kool, 1993b:fig. 21D); the central cusp of the rachidian tooth of *Acanthais* is much wider relative to the total rachidian width than the same cusp in *Acanthina*. This wide, well-developed central cusp is also present in *Thais nodosa* and *Neorapana muricata* (Kool, 1993b). In its denticulation, however, the *Acanthais* radula closely resembles that of *Stramonita haemastoma* ("floridana").

DISCUSSION

Relationships

Based on the radular and protoconch morphology, the nominal species *brevidentata* could be placed in *Stramonita*. However, the anatomy and shell ultrastructure (in addition to the overall shell morphology) are sufficiently dissimilar between *Acanthais brevidentata* and *Stramonita haemastoma* to warrant separate generic status for the former. *Stramonita* has a large bursa copulatrix in connection with and running alongside the capsule gland, and it has accessory salivary glands that are relatively much longer (one-third

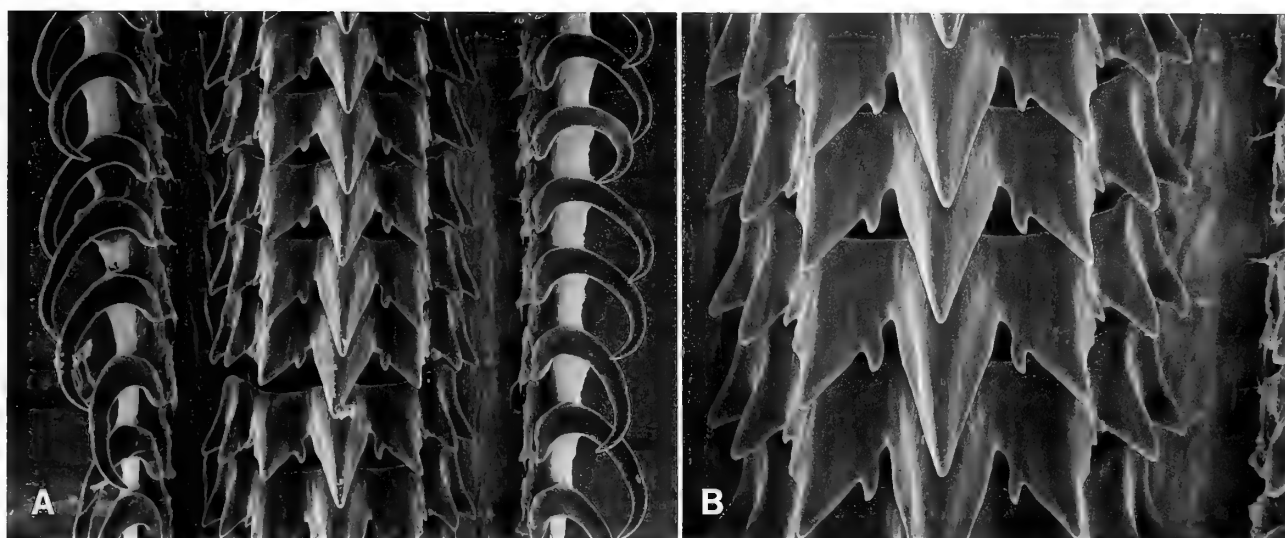


Figure 5

Radula, *Acanthina unicornis*, Talcahuano, Chile, MCZ 3717. A. $\times 450$. B. rachidian tooth, $\times 700$.

of shell height) than those in *Acanthina*. In addition to the differences in external shell morphology mentioned previously in this paper, *Stramonita* has a thick calcitic layer and one or two aragonitic layers.

From examination of an extensive suite of morphological characters taken from external shell morphology, protoconch, shell ultrastructure, operculum, anatomy, and radula, it is evident that *Acanthina brevidentata* should be taken out of the ocenebrine genus *Acanthina* and should be given a new generic name and placed in the Rapaninae (Thaidinae of authors; see Kool, 1993b).

Using characters of anatomy, protoconch, and shell microstructure, Kool (1993b) constructed a phylogenetic hypothesis of relationships in the Rapaninae. Incorporation into his analysis of results reported here for *Acanthais* shows that the latter taxon belongs to Kool's Clade G, which includes *Thais*, *Vasula*, *Neorapana*, *Tribulus*, *Mancinella*, and *Purpura*. Relationships within this clade were not resolved by Kool (1993b), but evidence offered in the next section implies that labral spines have evolved three times independently in Kool's Clade G (in *Acanthais*, *Mancinella*, and *Neorapana*).

We have chosen to propose the new genus *Acanthais* because the type species, *A. brevidentata*, does not readily fit into any named rapanine genus. An alternative solution would be to employ a single large genus *Thais* or *Purpura* for members of Clade G. Such a solution would, we believe, obscure relationships among distinct rapanine taxa. Regardless of whether *Acanthais* is accepted as a valid genus, the conclusion that it belongs to the Rapaninae and not to the genus *Acanthina* in the Ocenebrinae is strongly supported by an analysis of shell and anatomical characters.

Evolution of Labral Spines Within the Rapaninae

Short basal labral spines have evolved at least five times independently within the subfamily Rapaninae. They occur in *Acanthais* and *Neorapana* from the tropical eastern Pacific, *Concholepas* of the temperate southeastern Pacific, *Mancinella alouina* of the tropical Indo-Pacific, and several Indo-Pacific Miocene species of *Taurasia* Bellardi, 1882 (type species: *T. subfusiformis* (Orbigny, 1852), Miocene of southern Europe). The position of the spine is the same (basal to the fifth primary spiral cord) in *Acanthais* (Figure 1) and *Neorapana*, but differences in shell morphology and

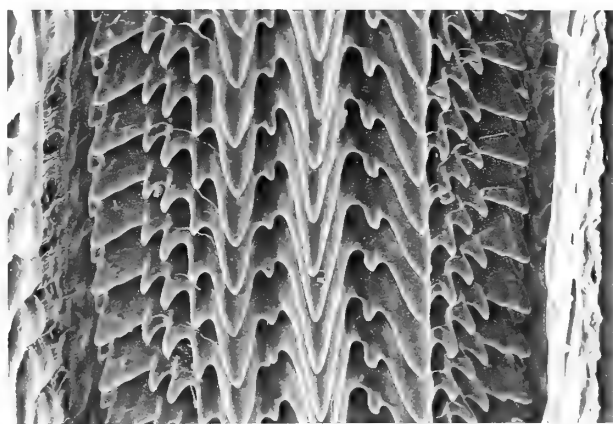


Figure 6

Radula, *Acanthinucella angelica*, $\times 900$.

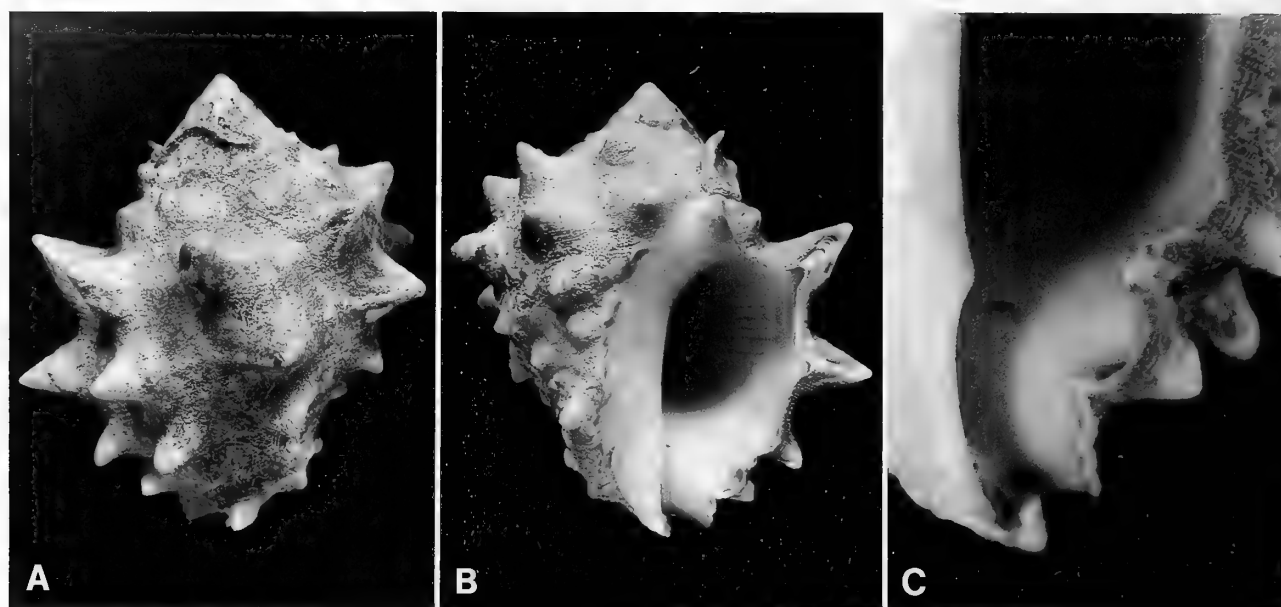


Figure 7

Shell morphology, *Mancinella alouina*, Nossy Komba, Madagascar, collected 27 June 1972. A. dorsal view, $\times 1.5$. B. apertural view, $\times 1.5$. C. basal portion of outer lip, $\times 4$.

anatomy discussed above imply that the labral spine evolved independently in these two genera. *Mancinella alouina* has the spine situated between the fourth and fifth primary cords (Figure 7), and is therefore likely to have evolved its spine independently of *Acanthais* and *Neorapana*. Some individuals of *M. alouina* lack a labral spine, as do other Indo-Pacific species of *Mancinella*. In *Concholepas*, the labral spine is very blunt, and usually consists of two adjacent protrusions instead of only one. This genus is phylogenetically close to the Australian and New Zealand genus *Dicathais* Iredale, 1936 (type species: *D. orbita* (Gmelin, 1791)) and is not close to the three genera mentioned previously (see Kool, 1993b).

Several Miocene species of the unusual genus *Taurasia* from Indonesia and the Philippines have a labral spine and an umbilical slit (see Beets, 1984, for a taxonomic review). The single living representative, *T. buccinea* (Deshayes, 1844), lacks a labral spine and has not been examined anatomically. Shell characters, including a parietal rib, place it in the Rapaninae, perhaps close to genera such as *Morula* Schumacher, 1817 (type species: *M. uva* (Röding, 1798), tropical Indo-Pacific) and *Muricodrupa* Iredale, 1918 (type species: *M. fenestrata* (Blainville, 1832), tropical Indo-Pacific); and *Cronia* H. & A. Adams, 1853 (type species: *C. amygdala* (Kiener, 1835), tropical Indo-Pacific). These genera have often been placed in the subfamily Ergalataxinae, but Kool (1993b) has shown that they form a clade within the Rapaninae. *Taurasia* has a straight columella with one or two central folds and several

ribblets basal to it. The outer lip is lirate within, and its apical end is extended as a gutter opposite the parietal tubercle. External sculpture consists of axial folds (sometimes confined to the early whorls) crossed by many scaly primary and secondary spiral ribs. Whatever the correct placement of *Taurasia*, it is clear that the labral spine evolved independently in this genus from the other four genera discussed above.

Labral spines in the Rapaninae are enlarged crenations on the edge of the outer lip that project ventrally more than do the other crenations. The tendency for one or more crenations on the basal part of the outer lip to be enlarged and to protrude ventrally is very widespread among members of the subfamily. It is well exemplified in several species of *Stramonita*, including the eastern Pacific *S. biserialis* (Figure 8), eastern Atlantic populations of *S. haemastoma*, and the Indo-Pacific *S. bitubercularis* (Lamarck, 1822). The enlarged crenations, which are often set off from the more adapical crenations by a space, are at the same position on the outer lip as is the labral spine of *Acanthais* and *Neorapana* (basal to the fifth cord). Some specimens of *Acanthais brevidentata* from throughout the geographic range of that species have an arrangement of crenations similar to that in species of *Stramonita* mentioned above, but one of the crenations is typically a little larger than the others and is equivalent to a poorly expressed labral spine. Other examples of enlarged and ventrally more projecting basal crenations occur in *Cronia avellana* (Reeve, 1846) and *Morula marginalba* (Blainville, 1832) from Aus-

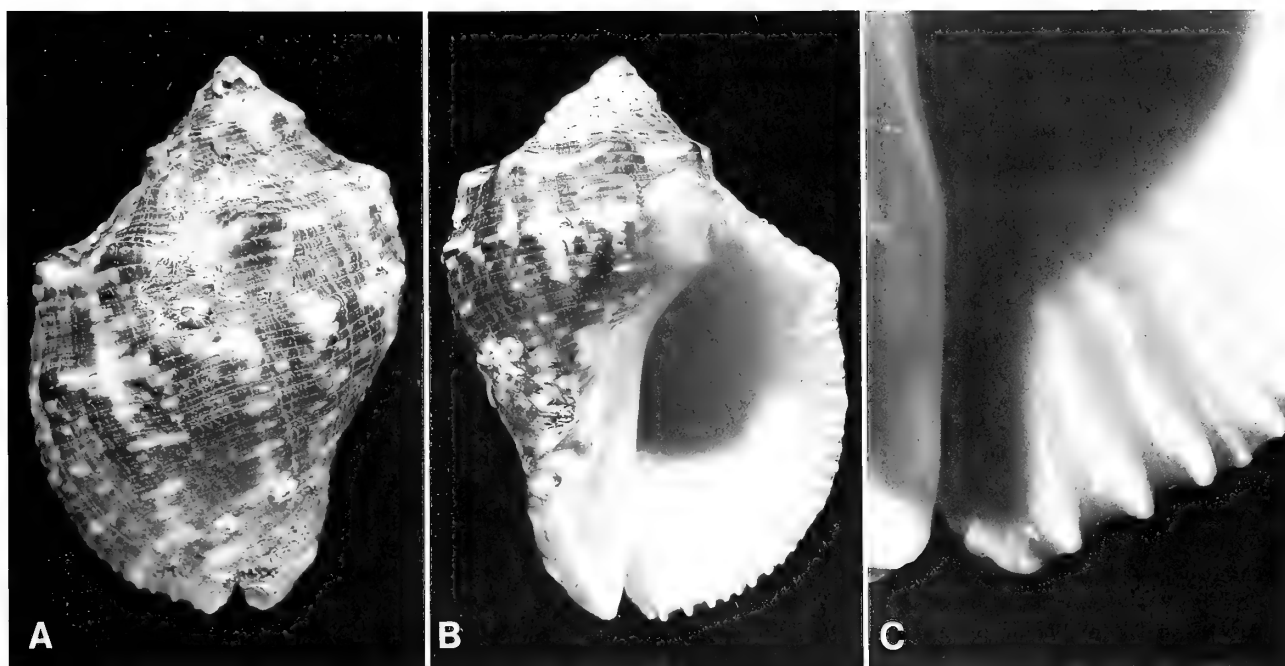


Figure 8

Shell morphology, *Stramonita biserialis*, Punta Caldera, Costa Rica, collected 3 July 1973. A. dorsal view, $\times 1.5$. B. apertural view, $\times 1.5$. C. basal portion of outer lip, $\times 4$.

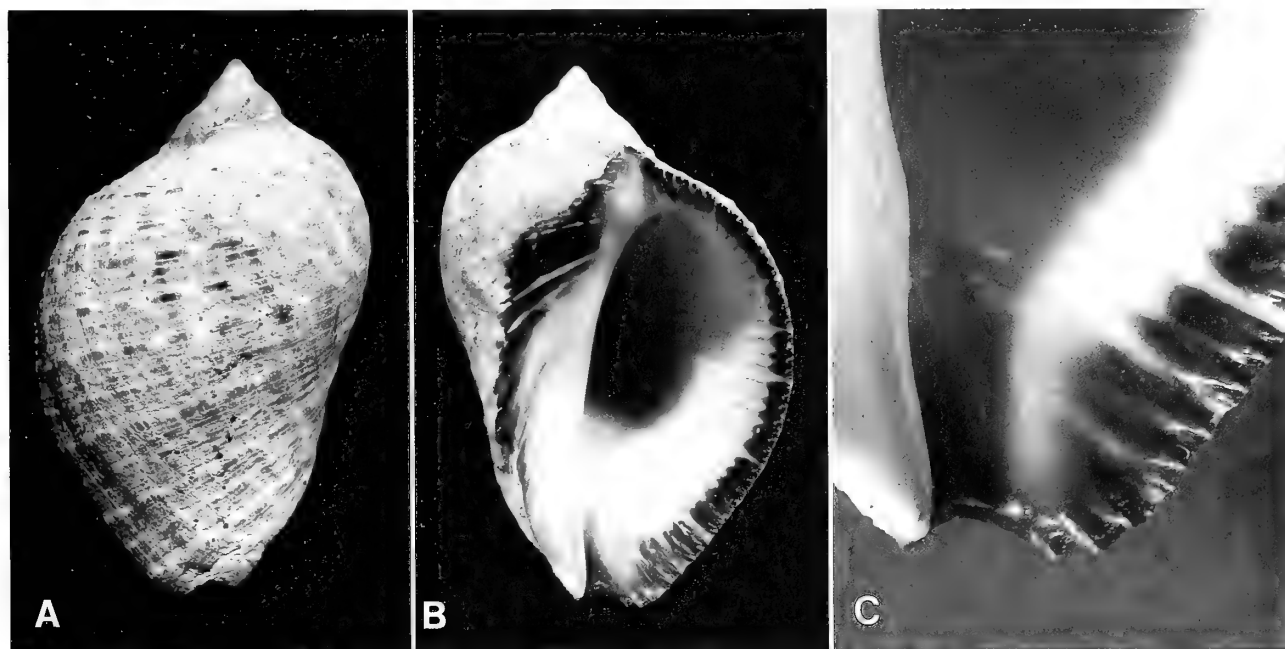


Figure 9

Shell morphology, *Purpura persica*, Guguan Island, Northern Marianas, collected 14 July 1981. A. dorsal view, $\times 1.5$. B. apertural view, $\times 1.5$. C. basal portion of outer lip, $\times 4$.

tralia, *Muricodrupa fenestrata* from the Indo-Pacific, *Thaisella lacera* (Born, 1778) from the Indian Ocean, and species of *Rapana* and *Purpura* Bruguière, 1789 (type species: *P. persica* (Linnaeus, 1758)) from the western Pacific (Figure 9). The labral spine is thus merely an exaggerated crenation, and it is not surprising that such a feature has evolved repeatedly and in the same position on the outer lip in several clades in the subfamily.

Given their identical positions on the outer lip basal to the fifth primary spiral cord, the labral spines of *Acanthais* and *Neorapana* are homologous. A superficial analysis would support a single evolutionary origin of this feature, but evidence from other characters indicates that the evolution of labral spines is parallel in the two genera. This case illustrates well the potential pitfalls of a superficial character analysis in phylogenetic reconstruction.

Biogeographical Remarks

Acanthais is one of at least nine endemic tropical eastern Pacific genera or species groups of common rocky-shore gastropods with no known living or fossil members outside the Panamic Province. These include the trochid *Tegula* Lesson, 1830; the turbinids *Callopoma* and *Uvanilla*, both of Gray, 1850; the muricids *Neorapana*, *Muricanthus* Swainson, 1840, and *Vasula* Mörch, 1860; the fascioliariid *Opeatostoma* Berry, 1958; and the siphonariid *Heterosiphonaria* Hubendick, 1945. Vokes (1990) considered *Muricanthus* to be a synonym of *Hexaplex* Perry, 1810 on the basis of the strong resemblance between the three eastern Pacific species of the group and the type species of *Hexaplex*, *H. cichoreum* (Gmelin, 1791) from the Indo-Malayan region of the Indo-Pacific. The three species of *Muricanthus* differ from all related species of *Hexaplex* in the New World and West Africa by the presence of a labral protrusion, and probably represent convergence in this character with the Indo-Pacific species such as *H. cichoreum* and *H. kusterianus* (Tapparone-Canefri, 1875). They therefore compose a distinctive endemic eastern Pacific clade. No fossil record is known for *Tegula*, *Acanthais*, *Opeatostoma*, or *Heterosiphonaria*. The other endemic groups are known back to the early Miocene (*Vasula*) or Early Pliocene (the other four genera) (see Durham, 1950; Woodring, 1959; Emerson & Hertlein, 1964; Vokes, 1990). Although the possibility that these groups once occurred in the western Atlantic cannot be ruled out, the available evidence indicates that significant genus-level evolution has taken place in the eastern Pacific since the uplift of the Isthmus of Panama during the Pliocene. It is striking that four of the groups (*Acanthais*, *Muricanthus*, *Neorapana*, and *Opeatostoma*) have evolved a labral spine. None of the western Atlantic relatives of these genera possesses such protuberances. These facts imply that evolutionary conditions in the eastern Pacific after the uplift of the isthmus have been very different from those in the western Atlantic.

ACKNOWLEDGMENTS

We thank J. H. McLean for the loan of specimens, and M. G. Harasewych and R. S. Houbrick at the Smithsonian Institution for the use of SEM facilities. E. H. Vokes and R. Houart made many useful remarks on an earlier draft of this paper.

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Spawn and Development of *Engoniophos unicinctus* (Say, 1825) (Gastropoda: Prosobranchia) from the Southern Caribbean Sea

by

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Abstract. The spawn and embryonic development of *Engoniophos unicinctus* are described. Each female spawns up to seven egg capsules measuring 4.4 ± 0.4 mm in maximum width, 1.4 ± 0.3 mm in minimum width (at the stalk area), and 4.8 ± 0.3 mm in height. Communal spawning was observed under laboratory conditions. Each capsule contains between four and 11 eggs measuring approximately $380 \mu\text{m}$ in diameter. An intracapsular veliger stage is reached between eight and 12 days after deposition. This veliger is characterized by a very large velum and a shell measuring $884.7 \mu\text{m}$ in length. Hatching takes place 18–20 days after oviposition, as non-swimming, crawling pediveligers measuring $1138.8 \pm 89.7 \mu\text{m}$ in shell length.

INTRODUCTION

Buccinids constitute a geographically widespread group of prosobranchs, and the reproductive biology of several species is known. In North America, the genus *Buccinum* Linnaeus, 1758, has received considerable attention (Martel et al., 1986a, b). In southern South America, Penchaszadeh (1971a, b, 1973) has studied the reproductive biology of several species of *Buccinanops* d'Orbigny, 1841. In the Caribbean, the spawn of *Antillophos candeï* d'Orbigny, 1842, and *Engoniophos guadalupensis* Petit, 1852, has been described by Flores (1978) and Bandel (1975) respectively.

The tropical buccinid *Engoniophos unicinctus* (Say, 1825) is very common in shallow waters of eastern Venezuela, where it is found living on soft bottoms and in *Thalassia*

testudinum beds. In this paper, the reproductive biology of *Engoniophos unicinctus* is presented.

MATERIAL AND METHODS

Specimens

Voucher adult material has been deposited in the American Museum of Natural History, New York, catalog number 232312.

Adult specimens and egg capsules were collected in February 1991 and 1992 (spawn masses are found in nature between February and September) at Isla Caribe, Chacopata, northern Araya Peninsula, Estado Sucre, Venezuela ($10^{\circ}42'11''\text{N}$, $63^{\circ}52'57''\text{W}$), between 0.5 and 4 m depth on sandy bottoms. Adults were collected using ham as bait. In nature, egg capsules are deposited on hard substrates such as empty gastropod and bivalve shells, dead coral, rocks, and *Thalassia testudinum* leaves. Adults were kept in aquaria at a temperature of 25–27°C in aerated,

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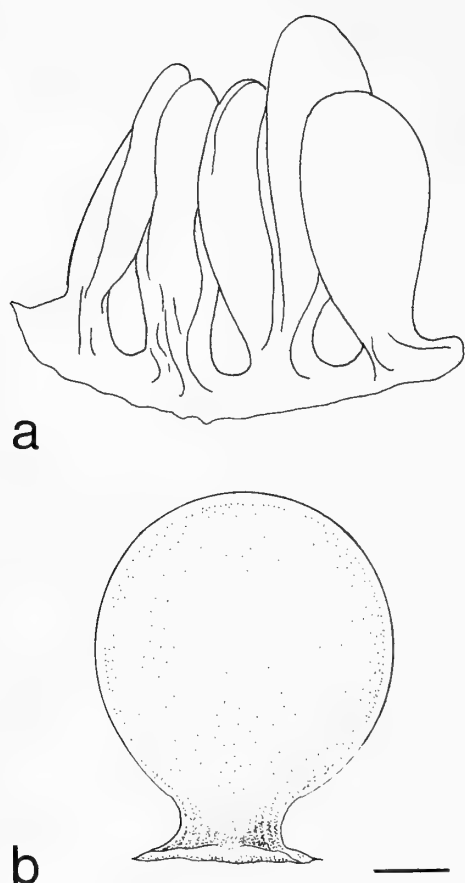


Figure 1

a. Spawn of *Engoniophos uncinatus*. b. Frontal view of egg capsule. Scale bar measures 1 mm.

non-circulating seawater. They were fed twice a week with ham.

Development

A total of 83 egg capsules collected from the field (1991), as well as 30 and 50 laboratory-spawned egg capsules (1991 and 1992 respectively), were examined. The following aspects of the spawn were studied: number and size of egg capsules laid per female, number and size of eggs and developing embryos within egg capsules, observations of the different stages of development, and time of embry-

onic development from egg to hatching. Observations were carried out with live material.

The egg and first division stages were observed under fluorescent light after previous fixation of the material for 12 hours with a glucamine-acetate (GA) buffer containing 4–6% formalin. This buffer was prepared with 250 mM N-metil glucamine, 250 mM K-gluconate, 50 mM HEPES, and 10 mM EGTA. The pH was adjusted to 7.4 with acetic acid. After fixation, the material was rinsed twice with GA buffer, and a third time with GA buffer containing 0.5 $\mu\text{g/mL}$ of the fluorochrome Hoechst 33258, which is a specific stain for the DNA. After 30–60 minutes, the samples were rinsed twice with GA buffer. Observations were carried out with a Leitz MPV 3 epifluorescence microscope equipped with appropriate filters for Hoechst fluorescent probes.

RESULTS

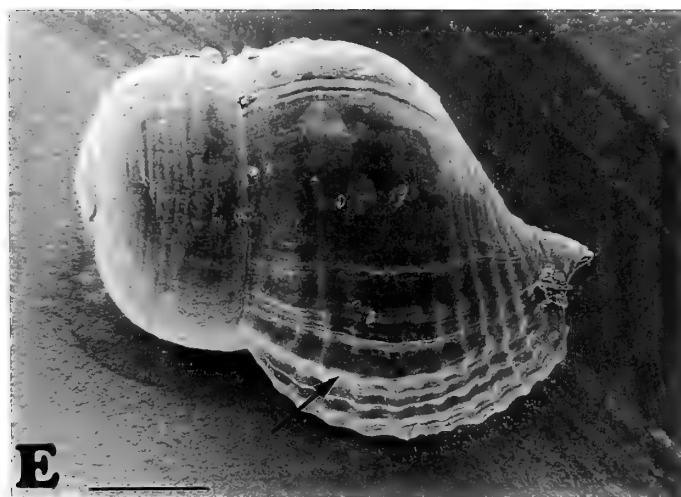
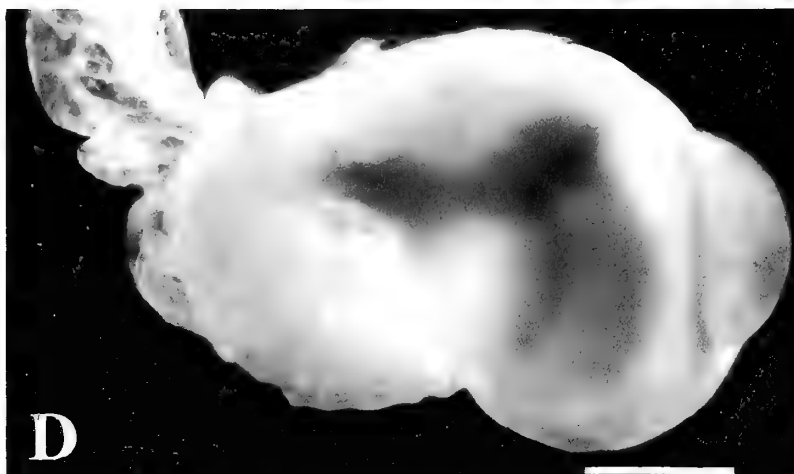
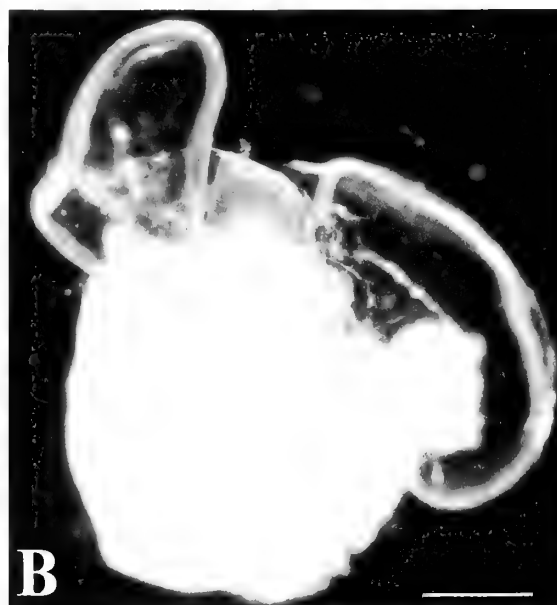
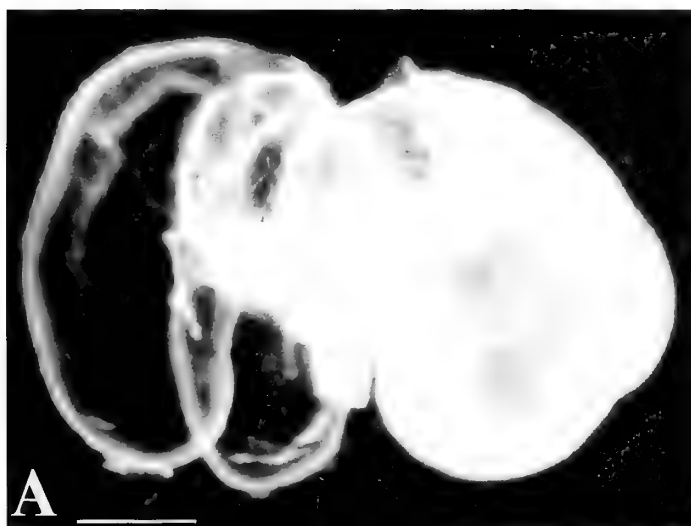
Sixty-four individuals were examined. Sexually mature males measured up to 20 mm (mean = 18.5 ± 1.0 , $n = 4$) in shell length, whereas females measured up to 28 mm (mean = 24.4 ± 2.4 , $n = 33$). In copulation observed in aquaria, the male was located on the upper part of the female shell. The penis was long, flattened, and gray. The copulating male attacked other approaching males with the proboscis. Also, a copulating female was observed depositing egg capsules at the same time. Total length of copulation was not recorded, but it lasted at least two hours.

Spawn masses of *E. uncinatus* (Figure 1a) were obtained throughout the year under laboratory conditions when females were being fed. In aquaria, females deposited egg capsules on the vertical glass surface. The egg capsules are oval-shaped with two flat sides fused together on the edges (Figure 1b). There is no pre-formed apical plate or escape aperture. The capsules are attached to one another by a basal membrane. Individual spawn masses were observed in the laboratory, each spawn mass formed of up to seven egg capsules. Communal spawn masses are common, and aggregations of two to three laying females were observed. In the field, egg masses were found between February and September. The aggregation of spawning females may result in a spawn mass of more than 50 egg capsules, which could also indicate a gregarious behavior for spawning in the field.

The egg capsules measure 4.4 ± 0.4 mm in maximum width (width at the center of the capsule), 1.4 ± 0.3 mm

Figure 2

Engoniophos uncinatus. A. Lateral view of the veliger larva (12 days). B. Frontal view of the veliger larva (12 days). C. Egg capsule with seven hatchlings prior to hatching. The two sides of the egg capsule are starting to separate from each other. Arrows indicate the velum remains of the hatchlings. D. Hatching stage showing the velum remains (18 days). E. SEM of the hatching shell; arrow indicates the area magnified in F. F. SEM magnification of the shell showing growth lines. All horizontal bars (A, B, D, and E) measure 250 μm . Vertical scale bar in C measures 1 mm.



in minimum width (width at the stalk area), and 4.8 ± 0.3 mm in height ($n = 49$ for all measurements). Capsules collected in the field in February 1991 contained at the early egg stage between four and 11 eggs each (7.6 ± 1.7 eggs/capsule, $n = 57$). Capsules spawned under laboratory conditions in February 1992 contained at the early stage between three and seven eggs each (4.9 ± 1.2 eggs/capsule, $n = 19$).

The eggs are yellow and measure $381.3 \pm 25.1 \mu\text{m}$ ($n = 85$) in diameter; they are embedded in a gel matrix. Observations under fluorescent light showed that the eggs are surrounded by follicular cells, which migrate to the animal pole before the emission of the first polar body and then detach from the egg. The first divisions of the fertilized egg in two and four cells occur within the first hours after deposition. At this stage, no follicular cells were observed. The two to four cell stage measures $475.8 \pm 59.3 \mu\text{m}$ ($n = 15$) in maximum length. An early veliger stage measuring $604.5 \pm 22.5 \mu\text{m}$ ($n = 4$) in length is reached in eight days. The late veliger stage, characterized by a very large bilobed velum, each lobe measuring between 1170 and 1248 μm in maximum length ($n = 4$), and a fragile, yellow shell, develops in 12 days. The shell of this intracapsular veliger measures $884.7 \pm 39.8 \mu\text{m}$ ($n = 57$) in length (Figure 2A, B). At this stage, some egg capsules, spawned at the same time and maintained in the same conditions, contain embryos at a prehatching stage. This prehatching stage is characterized by a well-developed foot with very small black dots, a smaller velum, and a stronger shell measuring $1007.5 \pm 61.7 \mu\text{m}$ ($n = 18$) in length. Hatching as a crawling pediveliger takes place in 18–20 days (Figure 2C, D). The foot (as in the prehatching stage), the mantle, and the siphon are pigmented with black dots. The velum is reduced, and no cilia are visible under the optical microscope; the pediveliger was never observed swimming. The shell is yellowish and measures $1138.8 \pm 89.7 \mu\text{m}$ ($n = 40$) in length (Figure 2E). There is no information regarding the moment in which the hatched pediveliger loses the velar remnants. The consistency of the gel matrix that surrounds the embryos is about the same throughout all developmental stages.

The pediveligers escape from the egg capsule by the opening of a portion of the suture that joins the two sides of the capsule, opposite the stalk. At hatching, the shell has two whorls, the first whorl lacking sculpture. The second one is characterized by several parallel growth lines (Figure 2E, F).

Capsules collected in the field in February 1991 and reared in the laboratory contained at the hatching stage between two and 10 pediveligers (mean 6.7 ± 2.1 , $n = 63$). This number is significantly different ($P < 0.01$) from the initial number of eggs per capsule (7.6 ± 1.7 , $n = 57$). No nurse eggs or cannibalism were observed. The capsules deposited and reared in the laboratory in February 1992, contained at the hatching stage between four and five pediveligers (mean 4.3 ± 0.5 , $n = 9$), this number not differing

significantly ($P > 0.05$) from the initial (4.9 ± 1.2 , $n = 19$). In several capsules, one small egg among normal-sized eggs or a very small pediveliger among normal-sized embryos were observed.

DISCUSSION

The observation that copulating females may be laying eggs simultaneously has been previously reported by Pearce & Thorson (1967) for the buccinid *Neptunea antiqua* (Linnaeus). The proboscis attack of the male toward approaching males has also been observed in the muricid genus *Phyllonotus* Swainson, 1833 (Roberto Cipriani, Universidad Simón Bolívar, personal communication) and in the buccinid *Buccinum cyaneum* (Miloslavich, personal observation).

Our observations on the spawn of *Engoniophos unicinctus* are very similar to those reported by Flores (1978) for what he called *Antillophos candei* and to those of Bandel (1975, 1976) for *Engoniophos guadalupensis*, which according to Abbott (1974) is a synonym of *Engoniophos unicinctus*. Because of the similarity of the spawn and the geographic localities, we believe that all observations correspond to the same species, which is *Engoniophos unicinctus*.

As in this study, Bandel (1976) reported that *Engoniophos guadalupensis* lays capsules in laboratory conditions all year round. Flores (1978) reported that egg capsules of *Antillophos candei* are found in the field between April and October. In this study, egg capsules were found in nature between February and September, possibly indicating a wider range in the spawning period than that reported by Flores (1978).

Both Flores (1978) and Bandel (1975, 1976) reported that their species hatched as crawling juveniles. Bandel (1975, 1976) specified that the developmental time from egg to hatching of *Engoniophos guadalupensis* was between 23 and 25 days, giving no information on the temperature at which the capsules were reared. In our study, development to the hatching stage was completed in 18 to 20 days at temperatures of 25–27°C, and hatching occurred as a crawling pediveliger. The veligers of *Engoniophos unicinctus* have a very well developed velum and when experimentally excapsulated, they freely move, using the velum as a motile organ. It would be interesting to follow the survivorship and development of the excapsulated veligers in order to determine if facultative poecilogony (as reviewed by Bouchet, 1989) is possible.

Concerning the number of developing embryos, there is a significant difference between the initial and the hatching stages that suggests that on the average one egg per capsule is disappearing. Nevertheless, no disintegration of any egg was seen (as in the case of the vermetid *Dendropoma corrodens* d'Orbigny, 1842, reported by Miloslavich & Penchaszadeh, 1992), nor was cannibalism between embryos noticed (i.e., no empty embryo shells).

Generally, tropical buccinid species do not have nurse eggs and hatch as veliger larvae [e.g., *Pisania pusio* (Linnaeus, 1758) and *Cantharus tinctus* (Conrad, 1846) reported by Bandel, 1975, 1976]. In temperate American buccinids, the presence of nurse eggs in species with direct development (or intracapsular metamorphosis) is a common feature. The North American species of the genus *Buccinum* complete their development with the ingestion of nurse eggs (Martel et al., 1986a, b; Miloslavich & Dufresne, unpublished data on *Buccinum cyaneum*), and hatch as crawling juveniles. The Pacific species *Searlesia dira* (Reeve, 1846) does not have nurse eggs, and the embryos uptake the albumen contained in the egg capsule fluid (Rivest, 1980). The studied southwestern Atlantic species of the genus *Buccinanops* all ingest nurse eggs through the course of development and hatch as crawling juveniles (Penchaszadeh, 1971a, 1973).

ACKNOWLEDGMENTS

We are especially indebted to Claudio Paredes from the Marine Biology Lab, Universidad Simón Bolívar, for his research assistantship in this work. We also thank the staff of the Unidad de Medios Audiovisuales, Universidad Simón Bolívar for their help with the photographs. This work was partially supported with a Decanato de Investigaciones, USB, grant.

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NOTES, INFORMATION & NEWS

The Collection of Recent Mollusks at the Paleontological Research Institution

by

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The Paleontological Research Institution (PRI) was founded in 1932 by Gilbert D. Harris, Professor of Geology at Cornell University from 1894 to 1934. Approaching retirement, Harris was concerned about the fate of his large fossil collections and library, as well as the continuation of his two journals, *Bulletins of American Paleontology* (begun in 1895) and *Palaeontographica Americana* (begun in 1916). He therefore founded his own scientific enterprise, erected a building for it behind his house, and received a charter as an educational institution from the State of New York in 1936. Harris retired as Director in 1951. He was succeeded by Katherine V. W. Palmer, who retired in 1977 at the age of 83. Peter R. Hoover was Director from 1978 to 1992, when he was succeeded by the current director. The Institution moved to its current location across Cayuga Lake from Cornell in 1968.

The PRI collections are best known for their richness in Cenozoic mollusks of the Western Hemisphere, especially the United States Gulf coastal plain, and the type and figured collection which includes more than 33,000 numbered lots (Brann & Kent, 1960; Fast, 1978). PRI has published a number of works on Recent mollusks (e.g., Perry & Schwengel, 1955; Olsson, 1961) and houses the figured specimens for these works, in addition to approximately 100 primary and secondary Recent mollusk types. Yet PRI has not previously been known as a major re-

pository of Recent mollusks. In late 1992, PRI began a reorganization (including physical regrouping by age and taxon and some initial curation) and preliminary inventory of its collection, apparently the first ever undertaken. (As part of its assessment of whether to move NY Route 96, the New York State Department of Transportation (DOT) in 1986 commissioned Shirley S. Albright of the New Jersey State Museum to make an estimate of the likely cost of moving the PRI collection. As part of her assessment, Albright made a preliminary inventory of the PRI collection. This information, however, was made available only to the DOT and its consulting engineers. The State has since made other arrangements for its highway relocation and there is no longer any threat to PRI.) In the process of this reorganization, it became clear that PRI houses a very large collection of Recent mollusks.

These collections are now grouped taxonomically and are accessible to visitors. A list of the number of lots held by family is available electronically by anonymous FTP from ucmpl.berkeley.edu, as document pub/mollusca/PRI-list, or by mail from the author. Particularly noteworthy are: (1) broad taxonomic and geographic coverage, with particular strengths in Florida and the Caribbean; (2) the large number of unionid bivalves (more than 21,000 specimens representing 108 species, including the federally listed endangered species *Dromus dromas* (Lea, 1834), *Obovaria retusa* (Lamarck, 1819), *Pleurobema clava* (Lamarck, 1819), and *Quadrula fragosa* (Conrad, 1835); and (3) the large number of pulmonate gastropods (inventory of pulmonates is incomplete, but the collection contains more than 3000 lots representing all major families). The collection also contains over 3500 lots of material with good locality data but no identifications. The entire collection includes at least 22,500 lots. This ranks it among the 20 largest in North America, according to data tabulated by Solem (1975).

Electronic supplements and appendices of papers published in *The Veliger* are available via anonymous FTP from ucmpl.berkeley.edu. These documents are available in three formats: PostScript (*.ps), WordPerfect (*.wpf), and ASCII (*.asc). To retrieve a document, open an FTP connection to ucmpl.Berkeley.Edu (128.32.146.30). At the request for login, enter "anonymous". At the request for a password, enter your e-mail address (e.g., jsmith@veliger.amu.edu). At the prompt, change directory to /pub/mollusca (command = `cd /pub/mollusca`), set file transfer mode to binary (command = `bin`), and retrieve the desired file (command = `get "filename.*"`). At the end of your FTP session close the connection (command = `close`) and quit. The electronic files associated with this paper are PRI-list.ps, PRI-list.wpf, and PRI-list.asc.

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International Commission on Zoological Nomenclature

The following applications were published in 1994 in Volume 51 of the *Bulletin of Zoological Nomenclature*. Comment or advice on these applications is invited for publication in the *Bulletin* and should be sent to the Executive Secretary, I.C.Z.N., %The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.

Case 2886 (Volume 51, Part 1, 30 March)—*Doris grandiflora* Rapp, 1827 (currently *Dendrodoris grandiflora*; Mollusca, Gastropoda): proposed conservation of the specific name.

Case 2870 (Volume 51, Part 2, 30 June)—*Xerophila geyeri* Soós, 1926 (currently *Trochoidea geyeri*; Mollusca, Gastropoda): proposed conservation of the specific name.

The following Opinions concerning mollusks were published on 30 June 1994 in Volume 51, Part 2 of the *Bulletin of Zoological Nomenclature*. Copies of these Opinions can be obtained free of charge from the Executive Secretary at the address given above.

Opinion 1765. *Fusus* Helbling, 1779 (Mollusca, Gastropoda): suppressed, and *Fusinus* Rafinesque, 1815 and *Colubraria* Schumacher, 1817: conserved.

Opinion 1766. *Tortaxis* Pilsbry, 1906 and *Allopeas* Baker, 1935 (Mollusca, Gastropoda): conserved by the designation of a neotype for *Achatina erecta* Benson, 1842.

Opinion 1767. *Pleurobranchus forskalii* Rüppell & Leuckart, [1828] and *P. testudinarius* Cantraine, 1835 (Mollusca, Gastropoda): specific names conserved.

Opinion 1768. *Taningia danae* Joubin, 1931 (Mollusca,

Cephalopoda): given precedence over *Octopodoteuthis persica* Naef, 1923.

Manuscript Reviewers for Volume 37 of *The Veliger*

The following outside reviewers contributed their time and effort to evaluate manuscripts submitted during the course of production of Volume 37. The quality of a journal such as *The Veliger* depends strongly on the (completely voluntary) service of independent reviewers such as these, and we are grateful to all of them.

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BOOKS, PERIODICALS & PAMPHLETS

The Cowry n.s.

JIRI ZIDEK, editor. Volume 1, number 1, 24 pp., quarto, May 1994. ISSN 0574-3737.

From the front cover: "*The Cowry* of Lt.-Col. R. J. Griffiths commenced in 1960 and ceased publication in 1968. It was devoted solely to the living Cypraeidae. The current journal honors Lt.-Col. Griffiths' effort by retaining the name and broadens his aim by encompassing the entire superfamily Cypraeacea and the related Velutinae. It is an international refereed journal that publishes both neontological and paleontological contributions on all aspects of the taxonomy, biology and phylogeny of these groups and accepts color illustrations. Contributions include, but are not limited to, original-research and review-type articles, short notes, pictorial accounts (variability, habitats, etc.), book reviews and literature notices." The editorial board includes members in the United States, New Zealand, Germany, and Holland.

Articles in the first issue include "Lt.-Col. R. J. Griffiths and his cowry journal" by J. Zidek and J. H. Black; "Catalog of fossil and Recent Cypraeidae and Eocypraeinae (Ovulidae) described since 1971" by L. T. Groves; "Beach-collecting cowries: possibilities and limitations" by W. Krommenhoek; and a section of editor's comments, including some words of gentle encouragement to potential contributors who may be uneasy about having their contributions reviewed by referees.

The journal evidently contemplates publishing descriptions of new taxa and requires that holotypes be deposited in public institutions and provided with catalogue numbers.

Frequency is semi-annual (May and November). An annual subscription is \$20 in the United States (\$25 elsewhere) for individuals and \$40 in the U.S. (\$45 elsewhere) for institutions. The journal is available from Dr. Zidek at P.O. Box 95, Socorro, NM 87801 USA (for subscriptions and correspondence), or at New Mexico Bureau of Mines & Mineral Resources, NM Tech C/S, Socorro, NM 87801 USA (for manuscripts).

B. Roth

Foregut Anatomy, Feeding Mechanisms, Relationships and Classification of the Conoidea (=Toxoglossa) (Gastropoda)

by JOHN D. TAYLOR, YURI I. KANTOR & ALEXANDER V. SYSOEV. 1993. *Bulletin of the Natural History Museum, London (Zoology)* 59(2):125-170.

The traditional family Turridae presents one of the most vexing problems in gastropod classification. It is enormously diverse, with more than 600 genera and some 10,000 Recent and fossil species described. This attribute and the prior reliance of taxonomists on few taxonomic characters have combined to inhibit the derivation of hypotheses of phylogeny by modern objective methodologies. It has long been recognized that this taxon needed to be subjected to a modern phylogenetic analysis based at least in part on anatomical characters, in addition to the shell and radular characters used in previous classifications. Not until completion of a broad survey of anatomy could there be sufficient evidence for changing the status of the numerous (11-17) subfamilies currently in use, although Morrison (1966) and McLean (1971) anticipated that changes in family-level classification would be the result.

Using information largely from their new comparative anatomical study of the foregut, Taylor, Kantor, and Sysoev have now presented the first phylogenetic hypothesis for the Superfamily Conoidea based on cladistic methodology. They also provide a detailed and well-documented basis for a revised classification of the family-group taxa previously assigned to the Turridae and to the other traditional families of Conoidea, the Terebridae, and Conidae. The rhynchodeum, proboscis, buccal mass, radular apparatus, and foregut glands provide 33 new anatomical characters, coded in 73 states. The authors present a cladistic analysis based on these and on 10 shell and operculum characters, the latter coded in 27 states.

Taylor, Kantor, and Sysoev diagnose the Superfamily Conoidea as having a venom gland and permanent rhynchodeum, the proboscis formed by elongation of the buccal tube, with the buccal mass located at its base, and a radular row primarily of five teeth but with the tendency to loss of the central and lateral teeth. They also provide a new classification of the superfamily, based in large part but not completely on their cladogram.

While a major accomplishment, the work under review is unfortunately difficult to use, partly because of its organization and partly because of the inherent complexity of the authors' task. To determine the characters that distinguish one family, subfamily or genus from another, the reader must work from the cladogram (with numbered nodes) and the new classification on p. 154, to the table of synapomorphies indicated by node number and character number (p. 153), to the tabular character analysis (p. 151), which decodes character and state numbers. A full character state matrix is given on p. 152. Taylor et al. illustrate 12 types of foregut morphology and then describe five types of feeding mechanism in Conoidea. The authors discuss representatives of each but the two sections are not well coordinated with each other, and they do not

explicitly indicate the distribution of these types among taxa. The new characters are generously illustrated, but the captions would have been more helpful had they indicated the family-group taxon of each genus illustrated.

Each family and subfamily in the authors' new classification is described in the section, "Diagnoses of Higher Taxa." These summarize shell, radula, and foregut characters but do not explicitly compare and contrast similar taxa in a way that would facilitate the challenging task of specimen identification. A table contrasts character states in the two subfamilies of Terebridae. Comparable tables for the reconstituted larger families Turridae and Conidae would have made the paper more user-friendly.

Because foregut anatomy constitutes their major contribution to the taxonomic database, Taylor et al. consider only the living Conoidea. In an appendix, they list all extant genus-group taxa and their new allocations. Type species and references for all Recent genera and subgenera described subsequent to Powell's (1966) monograph are given.

Although the Conoidea are well represented in Cretaceous and Tertiary strata, the work fails to mention the fossil record of any of the taxa. Of course such analysis would have to be restricted to the smaller set of shell characters, but it might have served to corroborate the phylogenetic analysis. Perhaps the authors intend to consider this at a later date. The omission of fossil genera in the appendix also impedes use of the new classification, because all available genera need to be taken into account when allocating taxa at the species level. An example is the omission of Olsson's (1964) Neogene genera from Ecuador, which Powell (1966) missed.

The phylogenetic tree of Taylor et al. incorporates vastly more information than the only prior cladistic analysis of the group, a primitive effort based solely on radular characters of turrid subfamilies and genera (Shimek & Kohn, 1981). In a particularly intriguing result, Taylor, Kantor, and Sysoev's phylogenetic analysis indicates that a widely considered characteristic feature of Conoidea, hollow marginal radular teeth that function as hypodermic needles to envenomate prey, originated independently at least five times in the evolution of this clade. We list these below, and we note their family-group status in the new Taylor et al. classification:

1. The large clade (indicated as Node 18 in Taylor et al.) including the subfamilies Coninae, Conorbinae, Clathurellinae, Oenopotinae, Mangeliinae, and Daphnellinae of the reconstituted family Conidae. (This clade also includes the subfamily Taraninae, interpreted as having lost the radula).
2. *Toxicionella* (Family Turridae, Subfamily Clavatulinae).
3. *Pilsbryspira* (Family Turridae, Subfamily Zonulispirinae).
4. Many members of the Family Terebridae.
5. *Imaclava* (Family Drilliidae). In cases 1–4 above, the

radula consists only of marginal teeth. In contrast, Drillidae retains the primitive radula character of five teeth per row fixed to a functional membrane. Hollow marginal teeth are an autapomorphy of the genus *Imaclava* and hence not shown in the Taylor et al. cladogram.

The new family-group classification of the Conoidea that Taylor et al. propose is quite unprecedented in that it ranks the Coninae as a subfamily of a family Conidae that includes other "higher turrid" subfamilies having hollow, hypodermic marginal teeth only and no radular membranes. Their summary argument is this:

Despite the distinctive shell form and high species diversity of the group, we have little anatomical evidence to support the separation of *Conus* at family-level from other higher turrids. We propose only subfamily status for the group. Every anatomical character-state of the conine foregut is shared with species of Clathurellinae and Conorbinae (p. 156).

However, in the section on results of their phylogenetic analysis (fig. 27), the authors state that:

Benthofascis (Conorbinae) and *Conus* (Coninae) (Node 27) share a number of characters. They lack an anterior sphincter to the buccal tube, but have an intermediate sphincter instead. Both have accessory salivary glands and retain an operculum. Additionally both genera show resorption of the inner shell whorls (p. 155).

But the Clathurellinae are noted in Table 3 as having one or two anterior buccal tube sphincters, lacking accessory salivary glands, and either having or lacking an operculum.

In their tabulation of synapomorphies for interior nodes of their cladogram, Taylor et al. (Table 4) indicate two for Node 27, accessory salivary glands present and teeth on the outer shell aperture lip absent. However, the character state matrix (Table 3) also indicates *Genota* to have the latter apomorphy which, if this is correct, should thus be assigned to the preceding Node 26. Like *Benthofascis* and *Conus*, *Genota* also has an intermediate rather than anterior sphincter, but unlike *Benthofascis* and most *Conus* species, it lacks an operculum.

Resorption of inner shell walls, mentioned in the section quoted above but excluded from the Taylor et al. analysis, has long been considered important in classification and the hallmark of the traditional family Conidae (d'Orbigny, 1852; Van Koenen, 1867). It served as a key character to distinguish subfamilies of Conidae in the classic monograph of Cossmann (1896). Inner shell resorption likely represents a suite of interrelated characters apomorphic in Conidae (Kohn, 1990), and its inclusion might strengthen the cladistic analysis.

The development of a formal classification from a phylogenetic hypothesis is always a step that requires subjective judgment. The classification proposed by Taylor et al. departs considerably from the cladogram. It explicitly includes information, mainly radular characters, from taxa

that could not be included in the cladistic analysis, because of the absence of anatomical information. In this classification, the Conoidea comprises the six families Drilliidae, Terebridae, Pseudomelatomidae, Strictispiridae, Turridae, and Conidae. Five of these are monophyletic according to the cladogram, but Turridae is both diphyletic and paraphyletic.

These problems are not readily resolvable, and the classification of the Conoidea remains in a state of flux. As next steps toward more satisfactory solutions we suggest exploring classifications based more closely on the results of Taylor, Kantor, and Sysoev's cladistic analysis than is their proposal, and enhancing their analysis by incorporating additional characters.

Alan J. Kohn
James H. McLean

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Reply by Dr. Taylor

We welcome the interest in our paper; the Conoidea are a fascinating group of gastropods and despite the disproportionate attention devoted to the shells of some of the taxa, our knowledge of relationships within the superfamily is very poor. We are very aware of the many inadequacies in our study, principally deriving from the fact that the Conoidea are such a diverse group, so that the species which have been studied anatomically represent only a small subsample of the total diversity. Primarily, we attempted to demonstrate that there are many features of the conoidean foregut which can be utilized in phylo-

genetic analysis. This information was obtained from serial sections of the proboscis and foregut of about 70 species of conoideans, integrated with information from previously published studies. Other organ complexes such as the reproductive system will likely yield further suites of characters but, as yet, remain uninvestigated.

Kohn & McLean advocate using more shell characters and fossil taxa in future analyses. However, we fail to see how the inclusion of fossils would corroborate the phylogeny as they suggest. Our work on turrids and terebrids has shown that shell characters are often a poor guide to internal anatomy. Recent studies of species of the subfamily Crassispirinae have highlighted the fact that animals with rather similar shells e.g., *Ptychobela*, *Funa*, and *Inquisitor* possess very different radulae and foregut anatomies (Kilburn, 1988, 1989; Taylor, in press). Additionally, some species placed in the Mangeliinae on the basis of shell characters turn out to have crassispirine anatomy (Kilburn & Taylor, unpublished). The problem is particularly acute in the Terebridae, where shells can be extremely similar but reveal quite different foregut structures e.g., *Terebra subulata* has a proboscis, hypodermic radula, venom gland, and accessory salivary glands, whereas *Terebra areolata* lacks all these structures. By contrast, a wide range of shell form is found within the Daphnellinae, but species share many common anatomical characters.

The authors highlight the fact that the classification we propose is not a direct transposition from the cladogram. We are of course conscious of the problems of developing a formal classification from the cladogram and very aware that some of the taxa we propose may be paraphyletic. As we were careful to point out (p. 157), the classification we propose represents a conservative compromise, and there are several reasons for this restraint. Primarily, the number of species we analyzed in the cladogram is only a small subset of the total diversity of conoideans, and new combinations of foregut structures are still being discovered (Kantor & Taylor, 1994; Taylor, in press). Moreover, the cladogram was not particularly well resolved or robust, and some nodes are supported by rather few, possibly weak characters. New and continuing work should help resolve some of these problems, although Arnold (1990) has suggested reasons why morphological phylogenies of some groups may never be well resolved.

Perhaps the feature of the classification which has vexed Kohn & McLean the most is the "downgraded" status of Coniinae. The *Conus* species that we have studied have a relatively underderived foregut anatomy (compared to, say, the Mangeliinae and Daphnellinae), which is very similar to that of species in the "borsoniine" group of our Clathurellinae. They have a buccal mass situated at the base of the proboscis, a single accessory salivary gland, acinous salivary glands, and a radular caecum. The venom gland is unchanged in histology anterior to the nerve ring, and the buccal lips are unmodified. The proboscis sphincter lies in an intermediate position within the buccal tube, but

this probably represents a posteriorward shift of the anterior sphincter to accommodate the long radular teeth of *Conus*. The snout gland, situated in the posterior of the rhynchodeum, may turn out to be an autapomorphy of *Conus*, but its distribution is unknown in conoideans other than those we have studied. As Kohn & McLean point out, internal shell resorption has in the past been used as a character to define the Conidae. We considered, but did not include this character in the cladistic analysis. Its inclusion would have made no difference to the structure of the cladogram except to add another apomorphy at the node of *Benthofascis* and *Conus*. Internal remodelling of the shell, involving both dissolution and deposition, is seen to a degree in many gastropods, and it is likely that *Conus* represents one extreme of this phenomenon.

John D. Taylor

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References in the text should be given by the name of the author(s) followed by the date of publication: for one author (Phillips, 1981), for two authors (Phillips & Smith, 1982), and for more than two (Phillips et al., 1983). The reference need not be cited when author and date are given only as authority for a taxonomic name.

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Hickman, C. S. 1992. Reproduction and development of trochacean gastropods. *The Veliger* 35:245–272.

b) Books:

Bequaert, J. C. & W. B. Miller. 1973. *The Mollusks of the Arid Southwest*. University of Arizona Press: Tucson. xvi + 271 pp.

c) Composite works:

Feder, H. M. 1980. Asteroidea: the sea stars. Pp. 117–135 in R. H. Morris, D. P. Abbott & E. C. Haderlie (eds.), *Intertidal Invertebrates of California*. Stanford University Press: Stanford, Calif.

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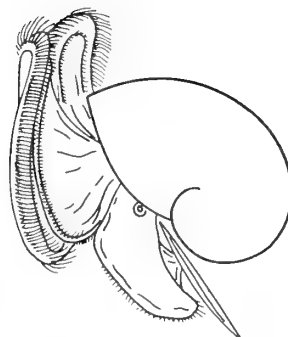
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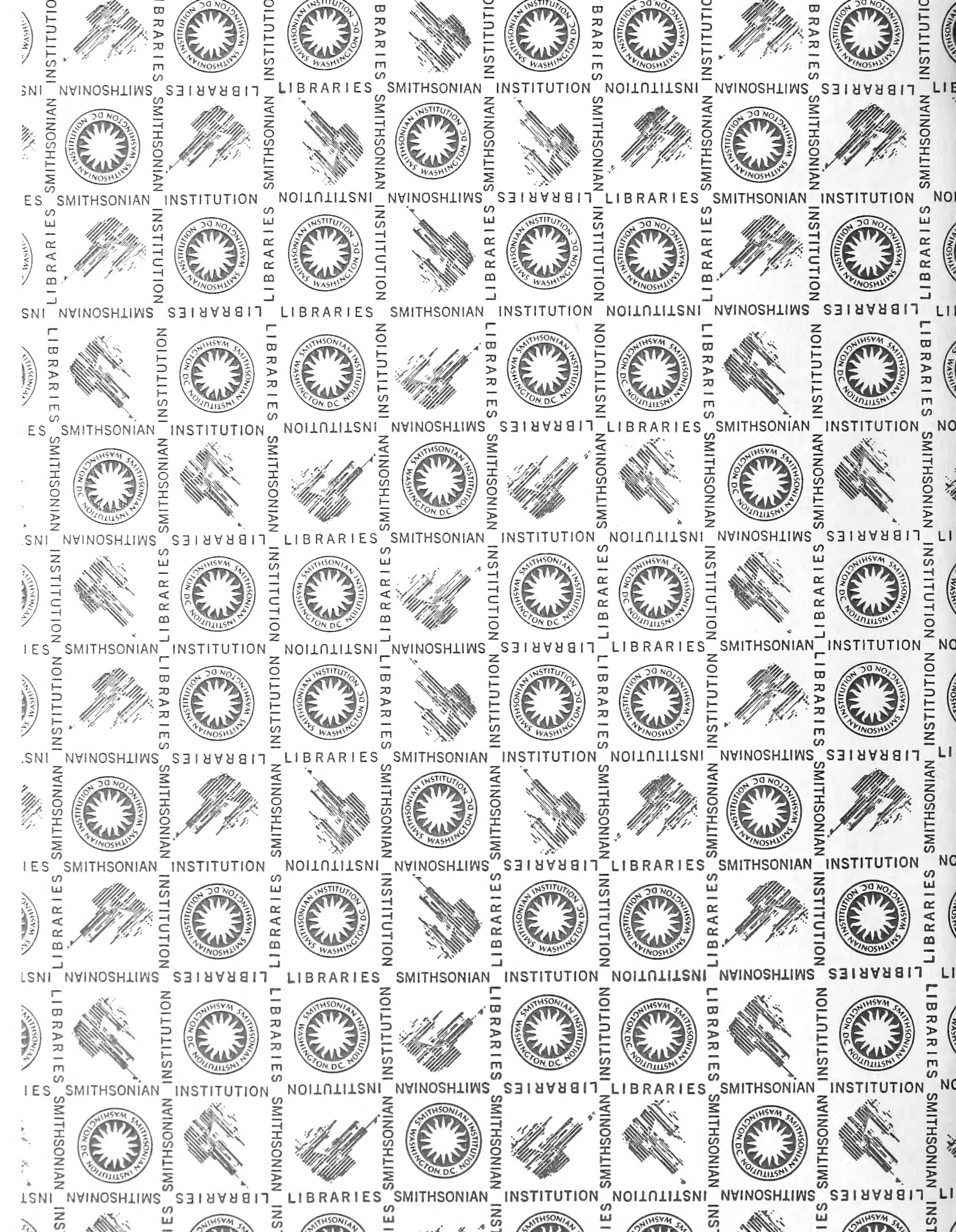
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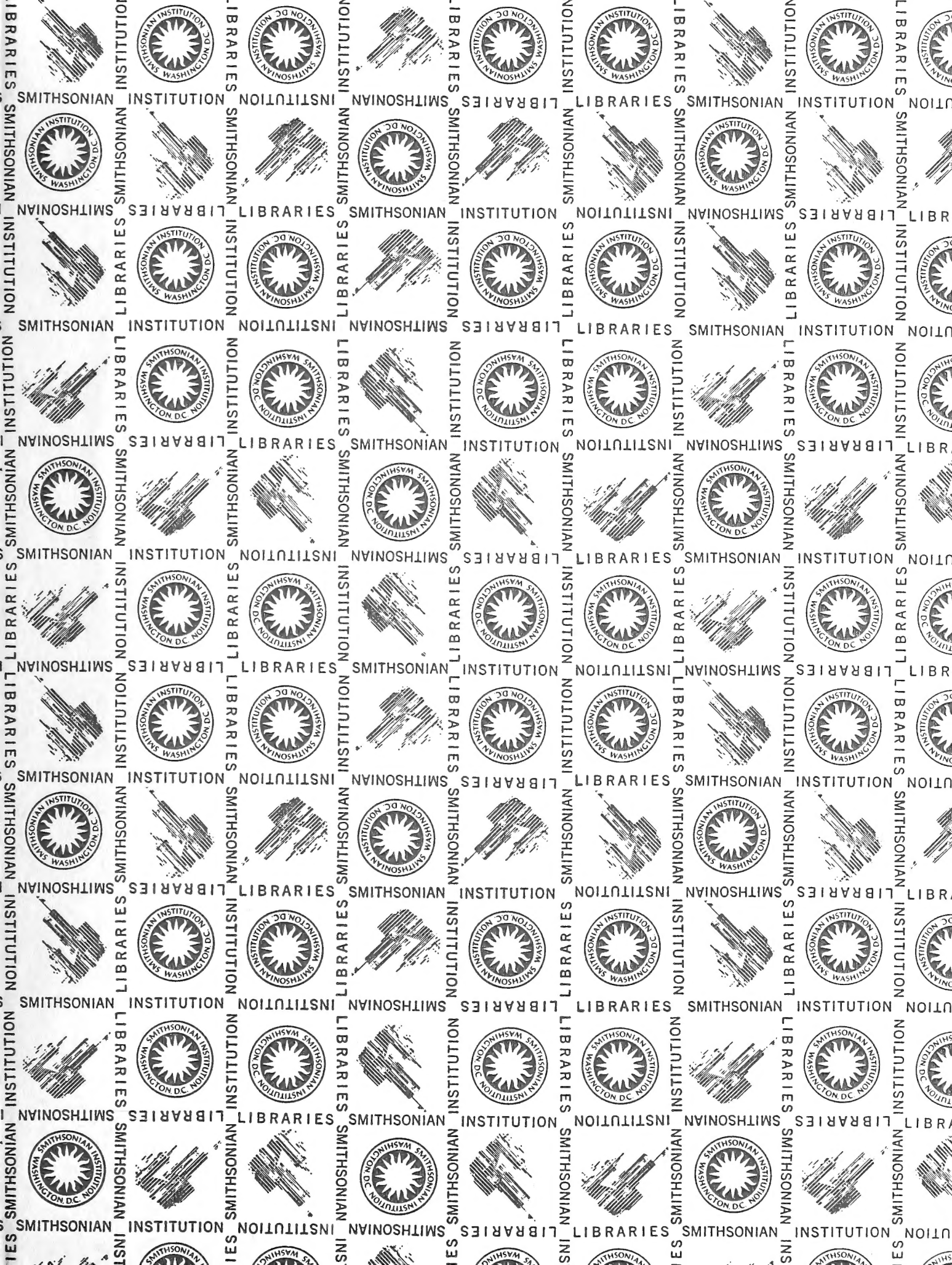
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